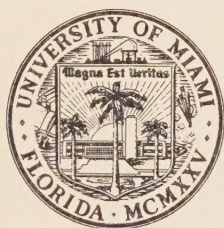


Bulletin of Marine Science of the Gulf and Caribbean

VOLUME 8, 1958
NUMBERS 1-4



Published by the University of Miami Press
ISSUED 1958 • CORAL GABLES, FLORIDA, U. S. A.



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BULLETIN OF MARINE SCIENCE OF THE GULF AND CARIBBEAN

VOLUME 8

1958

NUMBER 1

THE OCCURRENCE OF AMPHIBIANS AND REPTILES IN SALTWATER AREAS, AND A BIBLIOGRAPHY

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ABSTRACT

The paper discusses the occurrence of salamanders, frogs, turtles, crocodilians, lizards, snakes and one tuatara in the saltwater areas of the world. Previously published accounts are summarized, and new findings are also presented. At least 52 species or subspecies of amphibians, and 273 of reptiles, either dwell habitually in haline habitats or occasionally invade them. Such habitats are classified from a herpetological standpoint.

It is pointed out that, in Florida, a remarkably large number of essentially freshwater or inland species have also taken up residence in saltwater situations. An explanation of this circumstance is seen in both the geological history and the present ecological conditions of the state. Two areas of Florida—Merritt Island in Brevard County and the mouth of the St. Johns River in Duval County—are described as having an unusually large saltwater herpetofauna.

It is shown that residence in a saltwater habitat is apt to bring about changes in the coloration of an amphibian or reptile. Morphological changes may also be brought about; and diet is profoundly affected.

A bibliography of 475 titles is presented.

INTRODUCTION

The present paper is concerned with literature accounts and new records of amphibians and reptiles in sea water, in brackish ponds or lakes, on beaches, or in biotic communities controlled largely by salt water. Special attention is given to modifications of behavior necessitated by life in such areas; to peculiarities of structure or coloration seemingly induced by life in salt water; and to the ecological relationships of the saltwater species or populations.

In discussing the occurrence of amphibians and reptiles in saltwater areas, it is convenient to employ certain terms which should be explained. Six ecological "zones" are recognized herein: (1) The supratidal zone lies above high tide mark. Its flora consists largely of halophytes, and its pools of water are usually brackish to some de-

gree. The supratidal zone lies within reach of salt spray, at least during storms; and the distribution of the major plant species therein often is dependent chiefly upon resistance to wind-borne salt. (2) The tidal wrack zone usually consists of a narrow line of debris, lying at or just above high tide mark. It is generally composed of dead marine vegetation, leaves of halophytes, logs, and other plant material, cast upon the beach by high tides. Of course, in some areas a tidal wrack zone is lacking; however, when present it may provide shelter for certain cryptozoic species which otherwise could not exist in the vicinity. (3) The intertidal zone lies between the respective high and low tide marks. It is called the "upper neritic zone" by some authors. (4) The middle neritic zone is that area of shallow water lying just beyond low tide mark. Naturally, its width may vary greatly from place to place. In general, and with occasional exceptions, reptiles of the middle neritic zone are usually to be found in water of less than a meter's depth. (5) The lower neritic zone extends from the somewhat indefinite outer margin of the middle neritic zone to the edge of the continental shelf. This is an area of fairly deep water, rarely ventured into by the reptiles of the upper and middle neritic zones, but often visited by oceanic species. (6) The oceanic zone is the area of deep water lying beyond the edge of the continental shelf.

The above terminology is patterned after that recommended by the National Research Council's (1951) "Committee on a Treatise on Marine Ecology and Paleoecology," with, however, certain modifications. I have considerably restricted the meaning of the term "supratidal," and erected a "tidal wrack zone" for which the Committee felt no need. Any or all of the six zones may be called "saltwater areas," as contrasted with "inland areas" not affected by sea salt.

Herpetological taxonomy has not attained any remarkable degree of stability; various groups of species occasionally shift position in the taxonomic hierarchy. For present purposes, it seems to make little difference whether a certain group is called a family or a subfamily, a genus or a supergenus. Thus I have ignored some taxonomic quibbling and utilized what appears to be the most intelligible classificatory scheme. Scientific names are accompanied by common names, where such exist. The term "race," as employed herein, is synonymous with "subspecies"; this usage is customary in herpetology but not in some other sciences.

Although oceanic reptiles, such as the sea turtles, have been the subject of many papers, comparatively little attention has been

given to the herpetofauna of neritic waters, brackish ponds, and supratidal communities. Pertinent literature references are widely scattered. The only previous attempt to summarize this literature is that of Schmidt (1951a, 1951b), who presented an annotated bibliography of "marine ecological relations" of living amphibians, and a similar bibliography for living reptiles exclusive of turtles. Unfortunately, these bibliographies are extremely cursory. Thus, papers cited by Schmidt list among them only two amphibians and six reptiles from salt or brackish water areas of the United States; whereas at least 26 amphibians and 63 reptiles (exclusive of about 41 turtles) occur in such habitats within this country. A reconsideration of the subject is warranted.

Herpetological collectors often ignore saline waters and supratidal associations, devoting their attention instead to the supposedly more rewarding areas farther inland. No doubt, intensive field work would reveal many amphibians and reptiles about saltwater areas, in addition to those already known to occur there. The pan-tropical mangrove swamps dominated by *Rhizophora* and *Avicennia*; the Old World areas of firefly-mangrove (*Sonneratia*) and/or *Excoecaria*; the extensive *Nipa* swamps of the tropical Southwestern Pacific; the *Bruguiera*, *Pandanus*, and nutmeg-mangrove (*Myristica*) association of the New Guinean region, and the mangrove, *Derris*, and sedge association of that same territory; the Australasian sago (*Cycas*) swamps, which occasionally run from the fresh water into brackish; the strand communities which outline innumerable islands—all would doubtless repay further study. South America, especially, should yield additional saltwater species; it supports a large and varied herpetofauna about which little has been recorded. However, one need not go far afield to discover opportunities for research; the saltwater amphibians and reptiles of the United States are poorly known taxonomically, and almost unknown faunistically.

The invasion of saltwater areas by amphibians and reptiles is of special concern to workers in Florida, for the state appears to have an unusually large marine and brackish water herpetofauna. Reasons for this situation may be adduced. (1) The coast line of Florida is quite long, 1221 miles in length; of this, 714 miles outline the mainland and 507 miles surround islands. Thus, various salt and brackish water habitats are available for any species capable of invading them. (2) Most of the state is relatively low and flat; stream gradients are gentle,

and in many areas fresh water passes almost imperceptibly into salt. Presumably, inland species might gradually become adapted to coastal life, even though incapable of passing directly from freshwater habitats to salt. (3) Many inland lakes and streams of Florida, while not precisely brackish, contain an unusually large amount of dissolved chlorides—enough, in some cases, to permit invasion of inland waters by marine fishes, crabs, shrimp, amphipods, hydroids, and perhaps barnacles. This circumstance was discussed at some length by Odum (1953), who felt that such “oligohaline waters . . . are zones of evolutionary adaptive exchange between fresh and salt water” (p. 134). Odum was largely concerned with the invasion of fresh water by marine organisms, but suggested, “Gradual oligohaline gradients such as occur at the mouths of some oligohaline springs and the St. Johns River . . . should favor invasions and evolutionary adaptation of freshwater species to marine conditions” (p. 153). (4) The geological history of Florida may have favored the invasion of coastal habitats by inland species. During the Pleistocene there were marked fluctuations of sea level. At one time Florida was reduced to an archipelago; at another it extended outward about as far as the present edge of the continental shelf (Cooke, 1939). The reduction of the state to a series of small islands may have forced some species into saltwater habitats, or favored the survival of species that could exist in such places. In addition, extensive salt deposits were left in what is now inland Florida, and the gradual solution of these has resulted in the afore-said oligohaline waters. (5) The state lies athwart the boundary between temperate and subtropical regions, and also embraces portions of both Atlantic and Gulf drainages. This geographic location makes for a diversity of saltwater habitats: mangrove swamp, *Salicornia* flats, *Juncus* marsh, brackish pools of narrow-leaved cattail (*Typha*), a mangrove and shore-bay (*Tamala*) association, brackish sawgrass (*Cladium*) marsh, submerged fields of turtle-grass (*Thalassia*) and manatee-grass (*Cymodocea*), various strand communities, etc. The more saltwater habitats, the greater the likelihood that some species will find one of them congenial. (6) Finally, the state supports a large and varied herpetofauna. The more species present, the greater the chance that some will be able to thrive in salt water.

At least two localities in Florida support such an extensive saltwater herpetofauna as to warrant special consideration. These are Merritt Island, off the coast of Brevard County, and the mouth of the St. Johns River in Duval County. Studies at these localities afford some idea of

the ecological conditions under which the saltwater habitats may readily be invaded by inland species.

Merritt Island is bisected by the Banana River, a saltwater channel. The northern portion (which has no special name) is the only one under consideration here. This island is low and flat, with no freshwater streams. However, rainwater stands in ponds, bogs, and roadside ditches; and there is one deep hole, apparently an old limestone quarry, full of fresh water. The quarry hole is inhabited by the aquatic salamander, *Siren lacertina*, as well as by several species of freshwater fishes. The higher parts of the island support a growth of somewhat atypical rosemary scrub, an association generally considered to be the first timber stage following cessation of activity in coastal dunes. Twin-oak (*Quercus geminata*) and stunted longleaf pine (*Pinus australis*) are scattered about on the higher ground. A composite, sea ox-eye (*Borrchia frutescens*), is conspicuous at times. Here and there are hammocks of cabbage palm (*Sabal palmetto*), beneath which grow salt-bush (*Baccharis halimifolia*), wax-myrtle (*Myrica cerifera*), and a willow (*Salix* sp.). The periphery of the island is mostly salt marsh—broad flats overgrown with black-rush (*Juncus Roemerianus*), salt marsh grasses (*Spartina* spp.), glass-wort (*Salicornia perennis*), and salt-wort (*Batis maritima*). Channels leading into the salt marsh are bordered with narrow-leaved cattail (*Typha angustifolia*) and salt marsh leather fern (*Acrostichum aureum*), as well as *Juncus*, *Myrica*, and *Salix*. Black mangrove (*Avicennia nitida*) grows in scattered patches about the shores of the island. White mangrove (*Laguncularia racemosa*) is also fairly common, red mangrove (*Rhizophora mangle*) present but scarce.

Merritt Island is noteworthy for its water snakes, *Natrix sipedon*. At this locality a saltwater race, the Atlantic salt marsh snake (*N. s. taeniata*), intergrades with the freshwater Florida banded water snake (*N. s. pictiventris*), and also with the saltwater mangrove water snake (*N. s. compressicauda*). Search for these snakes, about the borders of the island, has revealed the presence of many other reptiles and a few amphibians.

On August 29, 1953, James M. Boyles and I visited Merritt Island, devoting special attention to the herpetofauna of saline waters. At one spot, southern leopard frogs (*Rana pipiens sphenoccephala*) were observed to jump into water that was too salty to drink. At the same spot were many young green tree-frogs (*Hyla cinerea*), clinging to the

stems of partially submerged black-rushes. When disturbed, they leaped into the water and out again. Narrow-mouthed toads (*Gastrophryne carolinensis*) were calling on a *Salicornia* flat at low tide; perhaps they had found some rainwater puddles. Little grass frogs (*Limnaeodes ocularis*) were calling from the stems of *Spartina* and *Acrostichum* bordering the brackish ditches, and Florida chorus frogs (*Pseudacris nigrita verrucosa*) from the ground in thick clusters of the halophytic grasses. A large Florida snapping turtle (*Chelydra serpentina osceola*) was collected on a tidal flat where diamondback terrapins (*Malaclemys terrapin tequesta*) had several times been taken. Chicken turtles (*Deirochelys reticularia*), striped mud turtles (*Kinosternon bauri palmarum*), and Florida mud turtles (*K. subrum steindachneri*) were common in brackish sloughs and ditches. Even the striped swamp snake (*Liodytes alleni*) was found crossing the road in an area of brackish water.

On this particular occasion, Merritt Island was flooded in consequence of recent heavy rains. Rainwater had filled the small ponds and ditches, had overflowed into the bogs and *Sabal* hammocks, and was pouring into the salt marshes. Undoubtedly, the heavy runoff and extensive flooding had disturbed some of the reptiles, causing them to move about and perhaps to invade areas which they would avoid under more usual conditions. Nevertheless, even during dry years the salt and brackish water herpetofauna of Merritt Island is surprisingly large, including *Rana pipiens sphenoccephala*, *Hyla cinerea*, *Kinosternon bauri palmarum*, and *K. subrubrum steindachneri*; the Florida soft-shelled turtle (*Amyda f. ferox*); the American alligator (*Alligator mississippiensis*); a king snake (*Lampropeltis getulus* subspecies); and the eastern cottonmouth moccasin (*Agkistrodon p. piscivorus*); in addition to the diamondback terrapin and the mixed population of *Natrix sipedon*. The last two normally inhabit the intertidal and middle neritic zones. One species of sea turtle, the Atlantic loggerhead (*Caretta c. caretta*), nests abundantly on the island, and other species are known from offshore waters.

At the mouth of the St. Johns River, reptiles and amphibians invade the brackish and salt water under a different set of conditions. The river flows northward a distance of nearly 200 miles, draining a low-lying area of innumerable lakes, ponds, and swamps. These bodies of water are generally covered, wholly or in part, with the introduced water-hyacinth (*Piaropus crassipes*). This plant forms great rafts or mats, portions of which break loose during times of high water and

float downstream. Reaching the mouth of the river, the plants pile up so thickly as to impede the progress of large vessels. Winds and tides force great masses of water-hyacinth back into the estuaries and tributary streams. The salinity of the water soon kills the plants. The decaying rafts of vegetation are sometimes carried out to sea, but often they rot in place.

These masses of dying *Piaropus* support a characteristic herpetofauna. The glossy water snake (*Natrix rigida*) is abundant in them. Also common are the rainbow snake (*Abastor erythrogrammus*), the cottonmouth moccasin (*Agkistrodon p. piscivorus*), and the Florida terrapin (*Pseudemys f. floridana*).

It might be argued that the reptiles were carried downstream with the water-hyacinths. It is true that reptiles may be borne on rafts of floating vegetation; Barbour (1920) found young of the striped mud turtle (*Kinosternon bauri*) in water-lettuce (*Pistia stratioides*) on the Colohatchee River of Florida, and Clench (1925) heard of an eastern diamondback rattlesnake (*Crotalus adamanteus*) which may have drifted to Sanibel Island, Florida, on a mass of water-hyacinth. However, I do not believe that rafting will account for the presence of many reptiles about the mouth of the St. Johns River. Freshwater *Piaropus* bogs of the St. Johns drainage are almost invariably inhabited by the black swamp snake (*Seminatrix p. pygaea*), the striped swamp snake (*Liodytes alleni*), and the mud snake (*Farancia abacura*), but rather seldom by the cottonmouth and very rarely by the rainbow snake and the glossy water snake. Nevertheless, at the river mouth, the usual hyacinth-frequenting species are absent, so far as is known, while the usual hyacinth-avoiding species are common. The saltwater rainbow snakes differ in coloration from those taken farther inland, a circumstance suggesting some degree of genetic isolation. The Florida terrapins from the mouth of the St. Johns are sometimes partly covered with large barnacles, betokening long residence in saline water.

The delta of the St. Johns has been settled by man. Marshes and swamps have been drained, tidal flats and estuaries filled in or otherwise altered by man's activities. The masses of water-hyacinth may provide concealment for reptiles which previously existed about the brackish marshes and streams. There is reason to believe that, before the introduction of *Piaropus*, the river mouth piled up at times with masses of water-lettuce and other native aquatic plants.

In Florida, the most extensive invasion of inland waters by marine species occurs in the St. Johns (Odum, 1953, p. 138). It is thus in-

teresting to note the considerable number of normally freshwater species in brackish situations at the river mouth.

There follows a discussion of the occurrence of amphibians and reptiles in saline waters, drawn from personal observation and from literature references. Thoroughly marine reptiles, such as the sea turtles, have been given somewhat cursory treatment. They have been mentioned in literally hundreds of papers; to include all the references would be to quadruple the bibliography without adding a great deal of information. No effort has been made to cite all the instances in which an arboreal species has wandered into supratidal vegetation, or in which a saxicolous species has followed a rocky outcropping to the edge of the sea. Such peregrinations probably involve little or no change in the habits of the animals involved. I have also omitted reference to a goodly number of speculative papers dealing with insular populations and the overseas distribution of terrestrial organisms. Purely taxonomic papers in most cases have not been included.

Before passing to the accounts of species, some papers of a general nature should be cited. Schmidt's bibliographies have been mentioned. Adolph (1927) discussed the physiology of adaptation to salt solutions in frogs, and provided a bibliography of pertinent references. Glaser (1875) supplied additional notes on the same subject. Brues (1927) pointed out that thermal waters and saline waters often are similar faunistically, and make similar demands upon the organisms that invade them. J. H. Davis (1940) discussed the ecology and geological role of mangroves in Florida. Davis was not concerned with the herpetofauna; nevertheless his paper is of value here as an account of the habitat to which several interesting reptiles are confined in Florida. This author (J. H. Davis, 1943) also described the natural features of South Florida, including the saltwater habitats, and provided notes on the American crocodile (*Crocodylus a. acutus*) and the sea turtles in this area. Eisentraut (1929) suggested that the melanism of certain Balearic lizards was due to a diet of halophytic plants rich in salts. Parker (1935) pointed out that, while metallic salts in the diet may in some cases serve to darken an animal's coloration, most instances of melanism are not the result of dietary factors. Mertens (1934) summarized theoretical considerations regarding the effect of sea salts and vegetable diet on the coloration of insular lizards. He also compared the fauna of continental and oceanic islands, discussed overseas dispersal of land animals, remarked on insular habitats, described the habits of certain littoral and marine lizards, listed the in-

sular lizards, and provided a bibliography. Schmidt (1930) discussed Pacific Island zoögeography, with special reference to the ways in which insular organisms reached their present locations, and cited a few records of lizards on beaches and in marine habitats. Williston (1914) provided a readable account of water reptiles, past and present. Woodbury (1936) described the fauna of Great Salt Lake, Utah. The salinity of this lake is near the saturation point, and no aquatic vertebrates live therein. However, a horned lizard (*Phrynosoma* species) is occasionally found on salty lakeshore flats. Ekman (1953) discussed the zoögeography of the sea, touching briefly upon marine reptiles; and F. G. W. Smith (1954) considered the taxonomy and distribution of sea turtles in a publication devoted to the origin and the fauna of the Gulf of Mexico. Strahan (1957) studied the effect of salinity on developing larvae of an Asiatic toad, *Bufo melanostictus*, which normally breeds in fresh water.

I am indebted to E. Ross Allen for his support of the study; to James M. Boyles and V. J. Allen for assistance in collecting; to William E. Brode and James R. Dixon for useful information; and to my wife, Joanne P. Neill, for assistance both in collecting and in readying the manuscript for publication.

DISCUSSION OF OCCURRENCE IN SALTWATER AREAS SALAMANDERS

Family AMBYSTOMIDAE.—Ambystomids are confined to North America. Some of the species burrow in the ground and migrate to ponds for breeding; others spend their lives in the water.

Schmidt (1951a, p. 43) stated that all amphibians known from brackish or salt water occur also in fresh. However, one ambystomid (*Ambystoma subsalsum*) is confined to brackish Lake Alchichica, in Puebla, Mexico. The water of this lake is salty to the taste, has no freshwater rushes or algae but only seaweed-like submerged plants, and but one species of fish (an endemic *Chiostoma*). Analysis of the water revealed total solids (mostly sodium, potassium, chloride, and bicarbonate) in a ratio of 8,283 p. p. m. (Taylor, 1943).

Large larvae of the British Columbia salamander (*Ambystoma gracile decorticatum*) were found in pools not far above high tide level on Goose Island, B. C. Some of the larvae were dead or dying, perhaps as a result of over-salinity (Carl, 1949). The species customarily breeds in fresh water. J. D. Hardy (1952) found spotted sala-

manders (*Ambystoma maculatum*) under driftwood at the edge of Chesapeake Bay. Ferguson (1956) found a larva of the Pacific giant salamander (*Dicamptodon ensatus*) beneath debris at the mouth of a creek about 20 feet from tidal wrack, in Lincoln County, Oregon. Spray from a nearby waterfall apparently neutralized any effect of sea spray. Weismann (1878) was under the impression that the axolotl (*Siredon mexicana*) inhabited brackish water, but he appears to have been in error (Taylor, 1943).

Family SALAMANDRIDAE.—The European newts (genus *Triturus*) are largely aquatic throughout most of their lives. Two of them, normally inhabiting fresh water, have also been reported in brackish. The common smooth newt (*T. vulgaris*) successfully breeds in brackish interdune pools, called "slacks," at Ainsdale, Lancashire, England (E. Hardy, 1943). Larvae of the palmated newt (*T. helveticus*) were found at Carradale Bay, Argyll, Scotland, in a brackish pool subject to invasion by sea water (Spurway, 1943, as *T. palmatus*). M. A. Smith (1951, p. 65) remarked of this species, "In coastal areas it has been found in water that is brackish, although what degree of salinity it can stand is not known. Oldham records that he has seen it in small pools so near the sea that in heavy storms they must receive a considerable amount of spray." Oldham (1933, 1934) has described the habits of this newt. Boulenger (1920b, p. 29) stated that it "has no objections to brackish water."

The American rough-skinned newt (*Taricha granulosa*) was found by Ferguson (1956) in a stream about 100 yards from the ocean in Curry County, Oregon. A high tide washed many of the newts about, and cast some of them up on the beach. A sea-washed specimen, rinsed in fresh water and kept captive, survived the experience.

Family PLETHODONTIDAE.—Dunn's salamander (*Plethodon dunni*) was found beneath debris at the mouth of a creek about 20 feet from tidal wrack in Lincoln County, Oregon (Ferguson, 1956). Spray from a nearby waterfall may have neutralized the effect of sea spray. This small salamander customarily dwells beneath damp humus and ground debris.

Family SIRENIDAE.—Sirenids are elongate, superficially eel-like salamanders; they lack hindlimbs. Gilled throughout life, they are thoroughly aquatic and normally inhabit freshwater situations. James R. Dixon (personal communication) found a western lesser siren (*Siren intermedia nettingi*) in brackish water near Hackberry, Came-

ron Parish, Louisiana. It was dead, and a bird was eating the carcass. Possibly the salamander had been transported some distance by a bird; however, there was brackish marsh for miles around. W. T. Neill, Sr., collected a greater siren (*S. lacertina*) near the mouth of the Pithlachascotee River in New Port Richey, Pasco County, Florida; the water was brackish, with numerous oyster bars. The siren may have come from a nearby drainage ditch in which the water was fresh.

FROGS

Family RANIDAE.—The so-called “true frogs” (genus *Rana*) are cosmopolitan in distribution. The majority of species live about fresh water or in damp situations. Most of them deposit eggs in fresh water, and these hatch into the small larvae known as tadpoles. A few species of *Rana* occasionally breed in saline pools, and the adults of many species are often capable of thriving in and about such waters. All of them are essentially inhabitants of freshwater areas, however.

The crab-eating frog (*Rana cancrivora*) of southeastern Asia usually lives about freshwater ditches, flooded ricefields, ponds and swamps. Nevertheless, it invades saltwater habitats with surprising frequency, as pointed out by Boulenger (1920a), Inger (1954), Loveridge (1945) and Mertens (1930). Annandale (1920) remarked, “Individuals are frequently found in brackish water, and I have seen one jump into the sea from a rock and swim ashore apparently without suffering.” Pearse (1911) made observations indicating that the tadpoles of *R. cancrivora* are able to live in strongly saline water. He found masses of tadpoles in crab burrows within the intertidal zone at Manila Bay, Luzon, P. I. Small frogs, 18 to 35 mm in length, also took refuge in these holes. Water over the burrows had a salt content of 2.6% by weight. (Normal sea water has a content of 3.5%.) M.A. Smith (1927) found this species in brackish water about river mouths in peninsular Siam.

The Asiatic species, *Rana limnocharis*, is often found in the brackish water of tidal creeks (Boulenger, 1912). According to M. A. Smith (1927, p. 7), *R. limnocharis vittigera* of the Philippines and *R. verruculosa* of the Timor Archipelago are closely similar to *R. cancrivora*; they are “never found many miles from the sea,” and may, like the crab-eating frog, be able to “enter salt water with impunity.”

The tiger frog (*Rana tigrina*) and the water-skipper (*R. cyanophlyctis*) were found in water with a salt content of 1.75% by weight,

near Port Canning, Lower Bengal, India (Annandale, 1907). Darwin (1899) probably had one of these species in mind, or perhaps *R. cancrivora*, when he stated that frogs and their spawn are killed by sea water except in the case of one Indian species.

The common frog (*Rana temporaria*), a well-known European species, was found breeding in brackish interdune pools at Ainsdale, Lancashire, England (E. Hardy, 1943). The edible frog (*R. esculenta*) and the lake frog (*R. ridibunda*) are well adapted to life about the Baltic Sea, which has a somewhat reduced salt content (Mertens, 1926). The latter species, a widely ranging one, has also been found in brackish water on the Ionian island of Santa Maura and at Budna, Dalmatia (Werner, 1909), as well as very near the beach near Bougie, Algeria (Bellairs and Shute, 1954).

A South American frog (*Rana palmipes*) was found on a beach in British Guiana, as well as in deep jungle (Crawford and Jones, 1933).

The southern leopard frog (*Rana pipiens sphenocephala*), one of the most abundant amphibians in Florida and other Southeastern states, has several times been reported in salt water. Its presence at Merritt Island has been mentioned previously. Carr (1940) listed it as being of occasional occurrence in salt marshes of Florida. Engels (1952) found it in small pools, presumably brackish, on the Shackleford Banks, North Carolina. J. D. Hardy (1953, as *R. pipiens*) remarked on its presence about the brackish waters of Chesapeake Bay, Maryland. Pearse (1911) reported it at Beaufort, North Carolina, in waters the salt content of which varied from about .02% to 2.14%. Liner (1954) found it in brackish waters of Terrebonne Parish, Louisiana. William E. Brode (personal communication) found it to be common about brackish marshes near Bay St. Louis, Mississippi, along with the pig frog (*R. grylio*) and occasionally the bronze frog (*R. c. clamitans*). Viosca (1923) stated that, in southeastern Louisiana, freshwater marsh merges gradually into salt marsh; and that the southern leopard frog, as well as the pig frog, both characteristic of freshwater marsh, were capable of resisting a limited amount of salt. James M. Boyles and I found many southern leopard frogs in salt marsh near the mainland end of the causeway leading to Cedar Key, Levy County, Florida. Numbers of them were hiding under an old boat which had been cast up on a black-rush flat. V. J. Allen and I found leopard frogs to be common along an arm of East Bay, Franklin County, Florida. The amphibians were concealed by halophytic reeds and grasses at the bay's edge. When approached, they leaped into

the water and out again. Blue crabs and a sting-ray were observed at the same locality. I also saw three of these frogs on the edge of a small pool within the intertidal zone at Green Point, Franklin County, Florida. When disturbed, they leaped into the water and were not seen to emerge.

A curious situation exists along the coast of southwestern Florida, with respect to the occurrence of the leopard frog in saline waters. From the general vicinity of Englewood southward to Cape Sable, in freshwater habitats back of the coast, typical *Rana pipiens sphenocephala* occurs. At certain localities about the brackish mangrove swamps, and occasionally in the freshwater habitats along with typical *sphenocephala*, one encounters a leopard frog perhaps worthy of taxonomic recognition. It is of gigantic size and robust proportions, dark in color, heavily spotted and vermiculated with blackish, and generally without the light tympanic spot characteristic of *sphenocephala*. J. A. Moore (1944, pl. 61, fig. 9) figured one of these frogs. Being unaware of their ecological and geographic restriction, and observing that they did not conform to the diagnosis of *sphenocephala*, Moore was erroneously led to conclude that the latter was too variable to merit recognition as a subspecies. Springer (1938) remarked on the gigantic size of leopard frogs from the area west of the Myakka River. Some of Springer's specimens were five inches in snout-vent length, weighing half a pound. They ate fiddler crabs (presumably in nature), and in captivity even devoured baby alligators.

The situation is complicated by the presence of yet another distinctive population of leopard frogs, far out in the very saline mangrove swamps near Cape Sable. Adults of this population are dwarfed, about 45 mm in snout-vent length, with a long and narrow head, very slender toes, a light tympanic spot, and a brownish coloration so dark as to render the dorsal spots obscure.

This is not the place to speculate about the taxonomic status of giant and dwarf leopard frogs in Florida. Suffice it to remark that the situation emphasizes the need for further herpetological study in salt-water areas.

Family BUFONIDAE.—This family is virtually cosmopolitan, one of its genera, *Bufo*, being absent only from Australia, New Guinea, Polynesia, Madagascar and, of course, Antarctica. *Bufo* species are generally called toads. Many of them are characterized by a tough, warty or granular skin. This anatomical peculiarity is usually thought to be

a factor permitting various *Bufo* species to inhabit relatively dry areas, although Thorson (1955) advanced a contrary view. Toads customarily migrate to the water for breeding and deposition of eggs. Rain-water pools are resorted to by many species; brackish water is frequented casually by some.

The natterjack toad (*Bufo calamita*) of Europe thrives about brackish as well as fresh water (Boulenger, 1897). E. Hardy (1943, p. 226) reported it as breeding in brackish interdune pools at Ainsdale, Lancashire, England, and commented, "The natterjack is, of course, a well known breeding inhabitant of brackish estuary waters . . ." Mertens (1926) considered this species well adapted to life about the saline waters of the Baltic Sea. Boulenger (1920b, p. 29) stated, "The natterjack toad . . . usually lives in colonies in sandy localities, such as dunes on the sea-coast, sand-quarries, heath-land, etc. . . . This toad shows not the slightest discrimination in the choice of water [in which to breed. It] has no objection to brackish water and is therefore often found in great abundance in close proximity to the sea. The greatest number I have ever seen was on the little Ile de Bast, opposite Roscoff, on which, for the reason that the pools are brackish, neither frogs nor the common toad exist." Mertens (1952a) remarked that the natterjack was common on coastal dunes of the North Sea islands. M. A. Smith (1951) observed that it was often found breeding in the storm-drenched brackish pools of the seashore. Additional comments are provided by Bell (1849).

The Old World green toad (*Bufo viridis*) sometimes breeds in brackish water (Boulenger, 1898; Mertens, 1952). It has been found about the Baltic Sea (Mertens, 1926), as well as in brackish waters of Algeria and Lower Egypt (Werner, 1909). Schmidt (1955) reported it from "among rocks above the beach" at Bushire, Iran. The widespread common toad (*Bufo bufo*) was found breeding in brackish interdune pools at Ainsworth, Lancashire, England (E. Hardy, 1943). An Asiatic toad (*Bufo raddei*) was discovered on the sea beach at Sikou, south of Chefoo, China. Specimens jumped into the sea and swam away from shore when disturbed (Shaw, 1934). Another Asiatic species (*Bufo melanostictus*) probably invades brackish water at times (Annandale, 1907).

An African toad (*Bufo mauritanicus*) was found under stones near a beach at Bougie, Algeria, probably in the supratidal zone. Tadpoles and metamorphosing toads, thought to be of this species, were abundant in streams crossing the beach and ending in shallow pools a few

yards from the sea. These pools were exposed to salt spray and concomitant increase in salinity (Bellairs and Shute, 1954). Doumergue (1901) remarked that in salty pools the tadpoles of *B. mauritanicus* feed upon glass-worts (*salicornes*).

A species of toad (*Bufo turpis*), occurring on Virgin Gorda in the British Virgin Islands, has been found under the loose bark of dead mangroves (Grant, 1932b).

It may be noted that a Neotropical toad, known scientifically as *Bufo marinus* and commonly as "marine toad," is not an inhabitant of brackish or salt water. Although occurring on coasts, it is essentially an inland species, and there appears to be no published record of its breeding in any but fresh water. E. Ross Allen (personal communication) found the species at the edge of Montego Bay, and on flats at the mouth of the Cabaritta River, Jamaica (to which island it has been introduced). At the river mouth, specimens were calling about ponds no more than 20 feet from the ocean. Probably these ponds were slightly brackish. Ely (1944) found that tadpoles of *B. marinus* placed in 15 per cent sea water (about .5 per cent salt content by weight) developed to metamorphosis. Water of this salinity seemed as favorable for development of the tadpoles as fresh water.

The southern toad (*Bufo terrestris*), a common species throughout Florida and the Southeast, was found by M. J. Allen (1932) beneath boards on the beach at Cat Island, off the coast of Mississippi. They had burrowed so far into the sand that only their snouts were exposed. Smith and List (1955) considered the species to be common about coastal meadows and offshore islands of Mississippi. I saw several large specimens hopping about at dusk on the beach near Bluffton, Beaufort County, South Carolina.

The oak toad (*Bufo quercicus*), also common in Florida and the Southeast, was noted on the beach at Harker's Island, off the coast of North Carolina; and on the nearby Shackleford Banks, Fowler's toad (*B. woodhousei fowleri*) not only occurred on the beach but even entered salt water when pursued (Engels, 1952). Fowler's toad also is found along beaches and on the coast of Texas (Wright and Wright, 1938). James R. Dixon (personal communication) collected specimens in salt marsh near Hackberry, Cameron Parish, Louisiana.

The Gulf Coast toad (*Bufo valliceps*) was found breeding in pools of the coastal marsh near Sabine Pass, Jefferson County, Texas; blennies were common in the same pools (Burger, Smith, and Smith, 1949). In Louisiana this species is sometimes associated with the

Gulf saltmarsh snake (*Natrix sipedon clarki*) about slightly brackish marshes (Viosca, 1926). James R. Dixon (personal communication) found *B. valliceps* in brackish marsh about 10 miles south of Hackberry, Cameron Parish, Louisiana. Specimens from this habitat were unusually blackish in coloration.

The California toad (*Bufo boreas halophilus*) was present at the sea coast in San Diego County, and was observed jumping into the sea at Benicia, Solano County, California (Storer, 1925). The subspecific names signifies "salt-loving." The red-spotted toad (*B. punctatus*), a species of Mexico and the southwestern United States, is also resistant to brackish water (Noble, 1931; Storer, 1925).

Family HYLIDAE.—The family Hylidae is cosmopolitan in distribution, and includes a large number of species scattered over many genera. Curiously, the only hylids reported from saltwater areas are certain ones occurring in the United States.

The hylid genus *Acris* is confined to North America, and the various named forms are currently listed as races of a single species (*A. gryllus*). This is the cricket-frog, one of the commonest amphibians in Florida and the Southeast. The coastal cricket-frog (*A. g. paludicola*) is known only from shallow pools of the coastal marsh near Sabine Pass, Jefferson County, Texas, where it was associated with blennies (Burger, Smith, and Smith, 1949). I observed the southern cricket-frog (*A. g. gryllus*) in shallow pools among sand dunes within 20 yards of the ocean in Bay County, Florida.

The genus *Pseudacris* includes certain small, terrestrial frogs of North America. The Florida chorus frog (*P. nigrita verrucosa*) was heard calling from salt marsh on Merritt Island, Brevard County, Florida, as mentioned previously. The spotted chorus frog (*P. clarki*) was found "in salt marshes very close to the ocean, in company with fiddler crabs" at Freeport, Brazoria County, Texas (Smith and Sanders, 1952, p. 208).

The hylid genus *Limnaoedus* includes only the little grass frog (*L. ocularis*) of the southeastern United States. Its presence in salt marsh at Merritt Island, Brevard County, Florida, has been mentioned.

The genus *Hyla* is cosmopolitan, and includes about 350 species. Most of them are arboreal, and are called tree-frogs. The United States species generally deposit their eggs in rainwater pools or the backwaters of streams. The green tree-frog (*H. cinerea*) was found about shallow pools of the coastal marsh near Sabine Pass, Jefferson County, Texas (Burger, Smith, and Smith, 1949). Carr (1940) listed it as

being "occasional" in mangrove swamps of Florida. Peterson *et al.* (1952) found it in brackish waters of the Florida Keys. Its presence in salt marsh at Merritt Island, Florida, has been noted. I also found it breeding in large numbers on the causeway across Mobile Bay, Alabama, in a supratidal habitat. Noble and Hassler (1936) found large choruses of this frog on sandy flats along Chesapeake Bay "where the water was in all probability brackish." J. D. Hardy (1953) mentioned the presence of the green tree-frog near Chesapeake Bay in Maryland, where it bred in ponds subject to salt spray and where salinities averaged 15 parts per thousand. A weakly differentiated population, once called *H. c. evittata*, is largely confined to the area of the upper tide-water Potomac River in Virginia (Dunn, 1937).

The gray tree-frog or "tree-toad" (*Hyla v. versicolor*) was observed in Chesapeake Bay marshes (Noble and Hassler, 1936); and the squirrel tree-frog (*H. squirella*) is said to range "to the very edge of the Gulf" in southeastern Louisiana (Viosca, 1923). The latter is common on the Florida Keys, and sometimes breeds in rainwater pools affected by salt spray. The pine woods tree-frog (*H. femoralis*) often breeds in brackish marshes near Bay St. Louis, Hancock County, Mississippi, in company with the green tree-frog, the squirrel tree-frog, and occasionally the barking tree-frog (*H. gratiosa*), according to William E. Brode (personal communication).

The Pacific tree-frog (*Hyla regilla*) inhabits western North America from Baja California to British Columbia. It frequents many habitats, from sea level to 11,000 feet, and normally breeds in freshwater situations. It was found by Murray (1955) on Cedros Island, off the coast of Baja California, where it was breeding in saline pools. Specimens from this locality were unusual in coloration.

The giant tree-frog (*Hyla septentrionalis*) is native to Cuba, but has been introduced into South Florida and appears to be spreading. On the Florida Keys it has been found breeding in brackish pools (Peter P. Kellogg, personal communication). Peterson *et al.* (1952) also found it in brackish water on Key Vaca.

FAMILY MICROHYLIDAE.—The microhylid toads are represented in both New World and Old. One species, the narrow-mouthed toad (*Gastrophryne carolinensis*), is common in the southeastern United States. It is secretive, burrowing beneath debris, and seems more or less independent of the major habitat boundaries. It usually breeds in transient rainwater puddles. It has several times been found in brackish

ponds. Its presence on a *Salicornia* flat at Merritt Island, Florida, has been noted. Peterson *et al.* (1952) found it in brackish water on the Florida Keys. It occurs in the brackish marshes of Chesapeake Bay (Noble and Hassler, 1936); J. D. Hardy (1953) considered it to have a "vigorous proclivity for haline habitats" in that area. Mansueti (1949), impressed with its ability to exist about salt water, suggested that it reached Maryland via the 1933 hurricane, for it was not observed in the state until 1936. J. D. Hardy (1953) opposed this view. Viosca (1923) reported the species on sea beaches in southeastern Louisiana. Werler and McCallion (1951) found two specimens under boards at the edge of a brackish marsh in Princess Anne County, Virginia. William E. Brode (personal communication) found the species breeding in water too salty to drink, near Bay St. Louis, Hancock County, Mississippi. James R. Dixon (personal communication) found it under boards in a salt marsh near Hackberry, Cameron Parish, Louisiana.

Family LEPTODACTYLIDAE.—The leptodactylid genus *Eleuthero-dactylus* includes a large number of medium-sized or small frogs, all of them confined to the New World and most of them Neotropical. They are noteworthy in that (so far as known) they do not spawn in the water, but deposit their eggs beneath stones, ground litter, and the like, or in epiphytic plants. One secretive species, the greenhouse frog (*E. ricordi planirostris*), has been introduced into Florida from Cuba, and now occurs at scattered localities from Key West to Jacksonville. On the Florida Keys it is often to be found under stones at the very edge of the sea. Another diminutive and secretive species (*E. luteolus*) has been found under coconut husks on dry sand within 50 feet of the beach at Negril, Jamaica, (Goin, 1953). Another Jamaican species (*E. jamaicensis*) was found under coconut husks, along with land crabs, in what may have been a supratidal situation near Montego Bay (Grant, 1939). On Antigua, B. W. I., *E. martinicensis* was found beneath stones and coconut trash on a beach (Lynn, 1957).

Family PIPIDAE.—A distinct suborder, the Aglossa, has been erected solely for the reception of the Pipidae, a family with one South American and two African genera. An African species, the clawed frog or platanna (*Xenopus laevis*), is aquatic, frequenting stream and pond bottoms. In the laboratory it was able to withstand a salt concentration of about 1.2 parts by weight (Rose, 1926). However, at a specific gravity "half way between sea and fresh water," it was "unable to leave the surface except by an effort" (Rose, 1950).

TURTLES—

Family CHELYDRIDAE.—The chelydrids are confined to the New World, a supposed New Guinean species proving to be nonexistent. The snapping turtle is represented in Florida by two races, the Florida snapping turtle (*Chelydra serpentina osceola*) in the peninsula, and the common snapping turtle (*C. s. serpentina*) in the northern portion of the state. The latter ranges over much of the United States and southern Canada, east of the Rockies. It occurs in brackish pools at the heads of tidal creeks on Ocracoke Island, North Carolina (Engels, 1942), and in the brackish waters of southeastern Texas (Guidry, 1953). Nichols (1914) also found it in brackish water. Babcock (1916) found it in Massachusetts salt marsh, where it fed upon a halophytic grass (*Distichlis*). The turtles, their stomachs full of this grass, appeared to be in good condition. The Florida race was found in salt marsh at Merritt Island, Florida, as mentioned previously. Usually the species inhabits freshwater streams, ponds, and lakes.

The alligator snapping turtle (*Macrolemys temmincki*), found from Florida to Texas and northward up the Mississippi Valley, is the largest freshwater turtle in North America. In Florida it is mostly confined to streams of the Gulf Coastal Plain, from the Suwannee northward, and to lakes along these streams. It feeds mainly upon fishes, which it lures into its mouth by means of a wriggling, worm-like appendage on its tongue, and preys to a lesser extent upon bottom organisms such as mollusks and crayfishes. Thoroughly aquatic, it rarely if ever leaves the water except to lay eggs. One might therefore expect it to enter the brackish or salt water rather frequently. However, the only published records of its occurrence in such habitats are those of Löding (1922) and of Haltom (1931, probably following Löding), who stated that it had been found in Mobile Bay, Alabama. On June 17, 1955, I saw a dead specimen on the causeway across this bay; it had been nearly decapitated, and probably had been caught by a fisherman in the vicinity.

Family KINOSTERNIDAE.—The Kinosternidae consists of four genera, all of them confined to the New World. The mud turtles (genus *Kinosternon*) and the musk turtles (genus *Sternotherus*) are small to medium-sized reptiles, largely carnivorous and scavenging, generally aquatic, and given to foraging on stream, pond, or lake bottom. The striped mud turtle (*K. bauri*) is confined to Florida. It was first found on Key West, where it was "tolerably abundant" in brackish ponds (Garman, 1891). It appears to be extinct on Key West today. Pope

(1939) said it thrived in "coastal brackish water." The presence of this turtle in brackish waters of Merritt Island, Florida, has been noted. Barbour (1920) found the young of this species "amongst floating water-lettuce in the Colohatchee River" of Florida. The circumstance suggests one way in which freshwater species might be carried into saltwater habitats. The eastern mud turtle (*K. s. subrubrum*) was found by Engels (1942) in slightly brackish pools at the heads of tidal streams on Ocracoke Island, North Carolina; and also (Engels, 1952) on the Shackleford Banks, North Carolina, where permanent fresh water is lacking. Carr (1952) remarked on its presence in "brackish-water creeks and estuaries." According to Conant (1945), it occurs in both fresh and brackish waters of the Delaware-Maryland-Virginia area. Babcock (1938) observed that it had been seen in brackish marshes. McCauley (1945) found it in certain "open brackish marshes" of Maryland. Pope (1939) remarked of the eastern mud turtle, "Brackish marshes are not avoided." Nichols (1914) found it in brackish water, where it was attacked by crabs. The Florida mud turtle (*K. subrubrum steindachneri*) occurs in brackish waters of Merritt Island, as stated previously. I collected the Mississippi mud turtle (*K. s. hippocrepis*) about brackish pools of the coastal marsh near Sabine Pass, Jefferson County, Texas.

The common musk turtle (*Sternotherus odoratus*) was found in the brackish waters of southeastern Texas (Guidry, 1953). However, like the mud turtles it is usually a freshwater reptile.

Family EMYDIDAE.—This family, also called the Emyidae, is virtually cosmopolitan, being absent only from the Australian faunal region. Many of the North American species inhabit freshwater lakes or streams, and some of these have occasionally been noted in saltwater areas. The spotted turtle (*Clemmys guttata*) is characteristic of small, shallow streams, and the edges of ponds and swamps. Nichols (1914) was probably the first to report its occurrence in brackish water. It was noted in brackish marshes of Maryland; it appeared to thrive in such places, although a few adult specimens collected there averaged smaller than those taken in fresh water (McCauley, 1945). Engels (1942) found it in slightly brackish pools at the heads of tidal creeks on Ocracoke Island, North Carolina. Pope (1929) stated that the spotted turtle was "often taken in salt marshes." Pope (1939) also remarked, "Brackish marshes are frequented. Individuals living in such marshes have rougher shells than those occurring elsewhere." The Pacific pond turtle (*C. marmorata*) normally inhabits ponds,

streams, and swamp margins, like its eastern congener. Pope (1939) stated, "Along the coast it enters brackish water, and Charles M. Bogert has even seen it at the edge of the sea far from the mouth of creek or river." Hurter (1912) found it to be common in a brackish slough near Laguna Beach, California. Stebbins (1954) and Carl (1951) mentioned its occurrence in brackish and sea water.

The emydid genus *Deirochelys* includes but one species, the chicken turtle (*D. reticularia*), an abundant reptile in Florida and other parts of the Southeast. It normally inhabits rather small, shallow ponds, especially those in pine flatwoods. Its presence in brackish water on Merritt Island, Florida, has been noted.

The emydid genus *Chrysemys* likewise includes but one species, the painted turtle (*C. picta*); four geographic races have been recognized, all of them usually inhabiting freshwater streams, ponds, lakes, and ditches. The eastern painted turtle (*C. p. picta*) is sometimes common in brackish tidal waters (Pope, 1939); and Babcock (1919) found specimens covered with a rusty deposit in New England salt marshes. Cochran (1952), Nichols (1914) and Stebbins (1954) remarked on the occasional occurrence of the species in brackish waters.

The emydid genus *Pseudemys* is confined to the New World. It includes about eight species, all of them normally inhabitants of streams, ponds, or lakes. They are popularly known as terrapins, cooters, sliders, or (in Florida) streaked-headed turtles. Three lines of descent may be recognized in this genus; it is convenient to speak of them respectively as the *floridana*, the *rubriventris*, and the *scripta* groups. Some of the members of the *floridana* group invade salt water with surprising frequency. The Suwannee terrapin (*P. floridana suwanneensis*) was noted long ago in brackish water by Knight (1871, as *Emys serrata*). He was impressed by the great numbers of these turtles around the mouths of streams emptying into the Gulf of Mexico south of Tallahassee, Florida. On one occasion he encountered these turtles to the number of "many thousands within the space of two or three acres, covering every log and stump and hummock almost as thickly as shingles lie upon a roof." Carr (1937b, 1940, 1952) discussed the habits of this turtle. It is abundant in clear spring-fed rivers of the Florida Gulf Coast, from Pinellas to Franklin County, and also in the turtle-grass and eel-grass flats off the mouths of these streams. Sometimes it wanders far offshore, and may be caught and taken to Cuba by visiting trawlers. Often, specimens are heavily covered with barnacles, a circumstance betokening long residence in

salt water. The populations on saltwater flats are naturally less susceptible to weather changes than the inland ones, and have been observed feeding when the air temperature was near freezing. In salt water, turtle-grass appears to be the main food. Pope's (1939) comments follow those of Carr (1937b).

In the vicinity of the Apalachicola River of northern Florida, the Suwannee terrapin intergrades with the closely related Mobilian terrapin (*Pseudemy floridana mobilensis*). The latter also invades coastal waters, including brackish estuaries, tidal flats, and saltwater flats behind offshore islands (Carr, 1940, 1952). M. J. Allen (1932, as *P. concinna*) found a dying specimen on the landward beach of Horn Island, Mississippi. He thought it had been carried out to sea and stranded on the island. Carr (1952) doubted that the salinity of the water was the cause of the turtle's decrepitude, pointing out that shrimp trawlers in former days caught many healthy Mobilian terrapins in the same sound. Several authors (Carr, 1940; Pope, 1939; Viosca, 1923) have reported "*Pseudemys alabamensis*" from, or even as characteristic of, brackish marshes. Apparently "*alabamensis*" is a mutation of *P. floridana mobilensis* and *P. f. suwanniensis* (Carr, 1938a, 1938b). It is interesting that the supposed mutation (involving the presence of a notch, flanked by cusps, at the tip of the upper jaw) appears to be associated with residence in brackish water.

Closely related to the Mobilian and Suwannee terrapins is the Florida terrapin (*Pseudemys f. floridana*). Unlike the other two, it is more characteristic of lakes and larger ponds than of streams. Its presence in brackish water at the mouth of the St. Johns River has already been noted. Some specimens are covered with barnacles, a circumstance demonstrating that their residence in a saltwater habitat is not a temporary one.

The *rubriventris* group is represented by the endemic Florida red-bellied terrapin (*Pseudemys nelsoni*). Usually this turtle inhabits streams, ponds, and lakes. It has been found along mangrove-bordered creeks in the southwestern portion of the state (Carr, 1940). Its more northern ally, the red-bellied terrapin (*P. rubriventris*), is likewise both fluviatile and lacustrine. Sometimes it occurs in the brackish lower reaches of streams, and in salt marsh (Carr, 1952; Pope, 1939). It has been taken in slightly brackish waters of the Delaware River (Conant, 1951).

Turtles of the *scripta* group also inhabit ponds, lakes, and streams. Apparently they almost never invade saltwater areas. Cagle and

Chaney (1950) found one specimen of the red-eared terrapin (*Pseudemys scripta elegans*) in a brackish canal at the Sabine Wildlife Refuge in Louisiana; usually, however, water in the canal is fresh. Baughman (1946) found this turtle in a Texas rice canal, in fresh water but associated with numerous marine fishes and crabs as well as freshwater fishes. Archie F. Carr stated (personal communication) that he had encountered an ornate terrapin (*P. s. ornata*) two miles out at sea and five miles from any river mouth, near a reef off Limón, Costa Rica. Apparently these are the only records of any member of the *scripta* group in salt water, unless the vague remarks of Bocourt (1868) relate to this complex. E. Waering (in Carr, 1952) reported the Baja California terrapin (*P. s. nebulosa*) in pools along the San Ignacio River; the water was said to be "brackish, due to the outcropping sandstone in the river bed." Such water would not usually be considered brackish.

On various islands of the West Indies (Cuba, Isle of Pines, Cat Island, Jamaica, Puerto Rico, Vieques, Hispaniola, Ile à Vache, and Great Inagua) are to be found more or less differentiated populations of the *scripta* group. Ten of these have received taxonomic recognition. All of them are closely related to *Pseudemys scripta ornata* of Central America, from which they may have been derived. Curiously, not a one of these turtles has been reported in salt water, although some, such as *P. felis* of Cat Island, are confined to areas where fresh water is of rare occurrence. Grant (1932a) was told by a resident of Vieques Island that, after severe hurricanes, *Pseudemys* had floated over from Puerto Rico on agglomerations of broken branches and limbs. Grant thought such an occurrence to be most unusual. Later, Grant, (in Grant and De Sola, 1934) kept five Puerto Rican terrapins (*P. stejnegeri*) in a tub of sea water for four days. Two of the turtles died the day after being returned to fresh water, and the eyes of all of them were impaired. It was concluded that "a very few miles of salt water would prove an effective barrier to these reptiles."

The emydid turtles of the genus *Malaclemys*, popularly known as diamondback terrapins, are noteworthy in being confined to brackish and salt water. The seven named forms are now all arranged as races of a single species (*M. terrapin*). Five of them reach Florida. The northern diamondback terrapin (*M. t. terrapin*) ranges (or once ranged) from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina. It is most characteristic of tidal creeks and estuaries in salt marsh. Occasional specimens venture into the open sea, or follow

coastal rivers upstream for considerable distances. The food consists primarily of mollusks and crustaceans; rootlets and shoots of marsh plants are occasionally eaten. The Carolina diamondback terrapin (*M. t. centrata*) ranges from Cape Hatteras southward coastally to northern Florida, being replaced on the lower east coast of the state by the Tequesta terrapin (*M. t. tequesta*). The optimum habitat of both these races is salt marsh, the turtles frequenting tidal creeks and estuaries, particularly over shell bottom and near oyster bars. The diet includes snails, other thin-shelled mollusks, and some plant material. The mangrove terrapin (*M. t. rhizophorarum*) inhabits the extreme southern coasts and Keys of Florida. It has been found around the islands in Florida Bay, and in hurricane pools on the Keys. As the common name suggests, it is generally associated with mangroves. Its habits are virtually unknown. Most of the Florida Gulf Coast is inhabited by the ornate diamondback terrapin (*M. t. macropsilota*). It frequents mangrove swamp, mangrove-bordered lagoons and creeks, salt marshes, and river mouths. The food consists mostly of thin-shelled mollusks, so far as is known. The Mississippi diamondback terrapin (*M. t. pileata*) ranges from the extreme western end of the Florida Panhandle along the Gulf Coast into Louisiana. Like the Atlantic races, it is partial to estuaries and tidal creeks; it is not particularly common over the shallow, grassy flats that lie along the Gulf Coast between the mainland and the offshore islands, although one might expect it in such places. Its habits have not been studied. The Texas diamondback terrapin (*M. t. littoralis*) is found coastally from western Louisiana at least to the Mexican border, and perhaps well into Mexico. Its habitat is much like that of *M. t. pileata*; its feeding habits are not known. There are verbal reports of diamondback terrapins in Mexican waters, but actual specimens are not at hand. Carr (1952) considered it possible that the species ranges all the way around the Caribbean coast to the Yucatan peninsula. The circumstance exemplifies the amount of work remaining to be done in salt-water habitats.

According to De Sola and Abrams (1933), most of the races of the diamondback terrapin are present on the Georgia coast between Savannah and Brunswick, for in this area a great many specimens had escaped from commercial terrapin farms and had taken up residence in the salt marshes there.

There appears to be no record of any diamondback terrapin in truly fresh water, although captive specimens can survive in this

medium. In nature the turtles sometimes range far upstream, but never, apparently, beyond tidal influence. Attempts to stock the species in fresh water have all failed.

For observations on the natural history of diamondback terrapins, see Cagle (1952a), Coker (1906a, 1920), W. P. Hay (1904), Pope (1939), and especially the summary of Carr (1952). Allen and Neill (1952f) briefly discussed the ranges, habits, and habitats of the Florida races, and figured a specimen of the ornate diamondback terrapin with a growth of oysters on its carapace.

During the latter Nineteenth and early Twentieth Century, the diamondback terrapin was highly prized as a table delicacy. The market price of these turtles soared, reaching \$90.00 a dozen. To supply the demand, many populations of the reptiles were virtually exterminated. This led to protective regulation of the terrapin industry, and to the establishment of "farms" where these turtles could be raised. A great many papers appeared, dealing with the biology of diamondback terrapins in captivity. Studies made by the United States Fish Commission, and its successor the Bureau of Fisheries, have been summarized by Anonymous (no date, b), Barney (1922), W. P. Hay (1917), Hildebrandt (1929), and Hildebrandt and Hatsel (1926). Other observations on captive specimens were provided by Coker (1906, 1920) and Hildebrandt (1932). The commercial importance of the terrapin industry has been considered by Schroeder (1924), Tressler (1923), and True (1884). Bibliographies have been provided by Anonymous (no date, a) and Ingle and Smith (1949). Other accounts contributing to the knowledge of *Malaclemys* ecology include Carr (1940), Finneran (1948), McCauley (1945) and Reid (1955).

Deraniyagala (1939) performed an experiment with a semiaquatic emydid turtle (*Geoemyda trijuga thermalis*) of Ceylon. According to him, this species avoids brackish water. When specimens were thrown into a brackish lagoon, they made for the mouth of a freshwater drain 20 meters away. Deraniyagala suggested that the turtles were able to ascertain the salt content of the water by "inhalation" (p. 268).

The common box turtle (*Terrapene carolina*) of eastern North America is terrestrial rather than aquatic, but sometimes immerses itself in mud and water. Latham (1916) found many box turtles in salt water on Long Island.

An Old World turtle of the genus *Emys* was found in salt water (Findenegg, 1951).

Family TESTUDINIDAE.—This family, as recently restricted, includes land turtles generally known as tortoises. They are herbivorous reptiles modified for life in comparatively dry surroundings. Giant tortoises (genus *Testudo*) were introduced onto Lignum Vitae Key, Florida, and one of them was found swimming in the ocean (Carr, 1952). The gopher tortoise (*Gopherus polyphemus*), a common species in drier areas of Florida, often occurs on offshore islands and old dunes, in dry supratidal situations. The Texas tortoise (*G. berlandieri*) was found in sand dunes along the beach near Port Isabel, Cameron County, Texas (James R. Dixon, personal communication).

Family PELOMEDUSIDAE.—The family Pelomedusidae appears to have no common name. It is represented in Africa, Madagascar, and South America. No pelomedusid has been reported definitely from salt water. However, Archie F. Carr (personal communication) was told by local residents that an aquatic snake (*Helicops* species) and a pelomedusid turtle (*Podocnemis* species) sometimes were carried into the bay at the mouth of the Orinoco River, Venezuela, amongst masses of drifting water-hyacinth. Carr personally observed the snakes but not the turtles. There is, however, no reason to doubt the record. The South American species of *Podocnemis* are large aquatic reptiles, mostly confined to the major rivers; three of them (*P. expansa*, *P. cayennensis*, and *P. vogli*) occur in in the Orinoco.

Family TRIONYCHIDAE.—These are the soft-shelled turtles, found in North America, Africa, Asia, and New Guinea. They are highly modified for aquatic life. The bony carapace is much reduced and covered by leathery skin; the resultant lightening permits unusual speed and agility in the water. Some of the species are known to carry on pharyngeal (and probably anal) respiration, enabling the reptiles to remain submerged for long periods. Some of the soft-shelled turtles are fluviatile; others thrive about almost any freshwater situation. The Florida soft-shell (*Amyda f. ferox*) occurs in ponds, lakes, and streams, and enters brackish water rather frequently. Carr (1940) listed it as "occasional" in the mangrove swamps of Florida. Carr (1952) also remarked that it "is not uncommon near the mouths of streams in brackish waters, where the tide must occasionally take it to sea"; and quoted Roger Conant to the effect that a specimen had been found at sea in Bahaman waters. I have seen Florida soft-shells at the mouth of the Pithlachascotee River, Pasco County, Florida, where the water is sufficiently saline to favor the growth of oysters; and have been told that commercial fishermen sometimes net these turtles from

the Indian River along with loggerhead sea turtles (*Caretta caretta*). The presence of the soft-shell in brackish water on Merritt Island, Florida, has been noted. Pope (1939), following Ditmars (1936), stated that the Florida soft-shell entered brackish water. Löding (1922) reported a soft-shell from Fig Island, Mobile County, Alabama; judging from the locality, it was the Gulf Coast soft-shell (*A. f. aspera*). Cagle and Chaney (1950) collected one soft-shell turtle in a brackish marsh of the Sabine Wildlife Refuge, Louisiana; as several races of *Amyda ferox* intergrade in this area, subspecific determination cannot be attempted.

A common Asiatic soft-shell (*Trionyx cartilagineus*), found usually in rivers, ponds, and swamps, also occurs in estuaries (De Rooij, 1915). An East Indian soft-shell (*Pelochelys bibroni*) is "often caught on the sea-coast," according to De Rooij (1915, as *P. cantori*). Boulenger (1912) also believed that it was found in coastal habitats, but M. A. Smith (1930) questioned its occurrence in such places. Nevertheless, Boulenger was specific; he said it was "not infrequently caught on lines of hooks set for sharks and rays. According to Cantor this turtle occurs in estuaries and on the sea-coast. At Penang it is frequently taken in fishing-stakes" (p. 12). Boulenger's reference is to Cantor (1847). The widespread distribution of this turtle (from the Philippines to southern New Guinea) suggests but does not prove some tolerance for salt water.

Family CARETTOCHELYIDAE.—This family includes but a single species, the pitted-shell turtle (*Carettochelys insculpta*) of New Guinea. It is a large reptile, attaining a shell length of 20 inches, and is generally described as being the only freshwater turtle with forelimbs modified into flippers like those of the sea turtles. It occurs in the Fly River and several other streams of Papua and Dutch New Guinea. According to De Rooij (1915), it follows the rivers "down to the sea," but it is usually thought of as a species of fresh water. Certainly it ranges far upstream, having been taken in the Strickland River. However, I was told by Malay and Chinese fishermen at Merauke, D. N. G., that this turtle also occurred at sea about the islands in the Papuan Gulf. An example from off the Merauke coast served to verify the identification. The species has been reported from Dameracura and Kiwai Island; these records are probably based on specimens collected in salt water. Almost nothing is known about the ecology of this remarkable turtle.

Family CHELONIIDAE.—The Cheloniidae (also called Chelonidae) includes four species, each placed in a separate genus and each consisting of two or more races. The cheloniids are known collectively as sea turtles; they display marked anatomical specializations for marine life, the most obvious being the modification of the limbs into paddle-like flippers. These turtles rarely visit land except to lay eggs; then the females venture onto sandy beaches to dig nesting holes. All four genera are represented in Atlantic waters, and occur off the Florida coast.

The Atlantic green turtle (*Chelonia m. mydas*) inhabits the Gulf of Mexico, the Atlantic Ocean, and the Mediterranean Sea. In American waters it ranges coastally as far north as Massachusetts and as far south as Argentina. There are unsubstantiated reports of the species in the Newfoundland region, also. At one time the Atlantic green turtle nested regularly on Florida beaches, and non-breeding specimens were plentiful along the coast of Georgia and the Carolinas; but today only stragglers are encountered so far north. This reptile is most characteristic of shallow neritic waters, especially those with a rocky bottom and an abundance of aquatic vegetation. However, the open sea is often visited; the species is still common about Ascension Island in mid-Atlantic. Remarks of early writers suggest that the green turtle formerly entered the short, spring-fed runs of Florida to feed upon the rich beds of *Sagittaria* and *Vallisneria* growing therein. The main foods are eel-grass (*Zostera*) and turtle-grass (*Thalassia*), although marine algae, jelly-fishes, mollusks, and crustaceans are occasionally eaten. For observations on the habits and habitat of the Atlantic green turtle, see Allen and Neill (1953), Audubon (1926), Carr (1940, 1942, 1954a, 1954b, 1956), Ditmars (1910, 1936), Duncan (1943), Garman (1884), Lewis (1940), Munroe (1898), Pope (1939), J. Schmidt (1916), True (1884), and especially Carr (1952) and Ingle and Smith (1949).

The Atlantic hawksbill turtle (*Eretmochelys i. imbricata*) inhabits the Gulf of Mexico, the Caribbean, and the warmer portions of the Atlantic, ranging northward to Massachusetts and southward to the Brazilian coast. There are unverified records for European and African waters, also. The hawksbill is most common in shallow coastal waters. Less restricted ecologically than the green turtle, it is sometimes found over mud bottom, and in areas where submerged vegetation is scarce or lacking. It eats both animal and plant food, perhaps favoring the former. Known items of diet include coelenterates,

mollusks, crustaceans, ascidians, and marine algae. The habits of the Atlantic hawksbill turtle have been discussed by Carr (1940, 1942, 1952), Ditmars (1910, 1936), Ingle and Smith (1949), Pope (1939), J. Schmidt (1916), and True (1884).

The Atlantic loggerhead (*Caretta c. caretta*) inhabits the Atlantic and the Mediterranean. On the American coast it has been found as far north as Nova Scotia and as far south as Argentina. It is the most nearly ubiquitous of the sea turtles, occurring in bays, inlets, estuaries, river mouths, and salt creeks, as well as in the open ocean. Sometimes it ascends rivers into merely brackish water. The loggerhead is largely carnivorous, feeding upon clams, oysters, sponges, jelly-fishes, and especially crabs and conchs. The Portuguese man-of-war, a stinging coelenterate, is also eaten. Fishes are occasionally caught. Plant foods include turtle-grass. For additional observations see Barbour (1926), Caldwell *et al.* (1955b), Carr (1940, 1942, 1952), Coker (1906b), Coles (1914), Daniel and Smith (1947), De Sola (1935), Ditmars (1910, 1936), Hildebrandt and Hatsel (1927), Hooker (1908a, 1908b), Ingle and Smith (1949), Murphy (1914), Pope (1939), and True (1884).

The Atlantic ridley turtle (*Lepidochelys olivacea kemp*i) is found in the Caribbean, especially the northern portion thereof; along the Atlantic coast of north America from the Florida Keys to Nova Scotia; about the Azores; and in waters of the British Isles. Unlike the other three species, the Atlantic ridley (so far as is known) rarely ventures into the tropical waters of the West Indies; it has been reported once in Jamaica and once in Cuba. It inhabits shallow coastal situations, often over marl bottom, and is especially characteristic of the red mangrove coast of western Florida. The feeding habits are not well known; spotted lady crabs (*Ovalipes*), Dolly Varden crabs (*Hepatus*), blue crabs (*Callinectes*) and gastropods are the only items reported from ridley stomachs. For observations on the habits of the Atlantic ridley turtle, see Aguayo (1953), Babcock (1930), Barbour (1942), Bleakney (1955), Carr (1940, 1942, 1952), Deraniyagala (1938), De Sola and Abrams (1933), Ditmars (1910, 1936), Dodge (1944), Dunn (1918), Garman (1888), Ingle and Smith (1949), Pope (1939), Schmidt and Dunn (1917), and Smith and List (1955). Deraniyagala (1957) suggested that the Atlantic ridley frequently nests near Miami, Florida, but the hatchlings which he examined actually were purchased in Veracruz, Mexico (Fugler and Webb, 1957).

The apparent absence of the ridley from Caribbean waters merits additional comment. The species is fairly common along the Gulf shores of Florida, and in fact may reach its maximum abundance around Florida Bay (Carr, 1942, 1952); yet there are only two Caribbean records, one for Jamaica (Dunn, 1918) and one for Cuba (Aguayo, 1953). The turtle seems to be unknown in the Bahamas (Carr, 1952), and C. B. Lewis (1940) doubts its presence in Jamaican waters. The Cuban specimen described by Aguayo is of considerable interest. The Atlantic ridley is very consistently gray in color, and almost always displays five laterals; but Aguayo's example was grayish olive above, and the laterals number seven on at least one side of the body as may be seen from Aguayo's photograph. Now Pacific ridleys are characterized by an olive coloration and laterals in excess of five. The circumstance leads to speculation as to whether a few ridleys might have crossed the Atlantic from Africa to the Caribbean. The species has been reported for South Africa and West Africa, although little is known about its presence in these areas. Obviously, any ridleys that turn up in Caribbean waters should be carefully examined and compared with the known populations of *Lepidochelys olivacea*.

All four species of cheloniid sea turtles once nested on the Florida coast, but today the loggerhead is the only one to do so with any frequency. Adults of the loggerhead and the ridley are fairly common in Florida waters, those of the green turtle and the hawksbill somewhat less so. Sea turtles appear to have dwindled in numbers largely as a result of man's activities. The capture of nesting females, the erection of buildings along so many beaches, and the netting of specimens at sea—all may have contributed to the decline of these reptiles.

Apparently sea turtles wander, at least occasionally; a specimen caught off Cape Hatteras may have been hatched on an island in Central American waters. Indeed, it is likely that most West Atlantic sea turtles were hatched somewhere about the Caribbean or the Gulf of Mexico, there being today comparatively little breeding activity outside these areas. Therefore, as Ingle and Smith (1949) have pointed out, effective conservation of the West Atlantic sea turtles is possible only with the cooperation of all the countries bordering or lying within the Gulf-Caribbean area. Carr and Caldwell (1956) have described a project to acquire the natural history data needed for intelligent management of a sea turtle industry.

The four genera and species of cheloniid turtles occur likewise in Pacific waters. The East Pacific green turtle (*Chelonia mydas agassizi*) is found along the tropical Pacific coast of the Americas. Another race, the West Pacific green turtle (*C. m. japonica*), has been recognized from Asiatic waters. The Pacific hawksbill turtle (*Eretmochelys imbricata squamata*) is said to occupy the tropical west coast of the Americas, and also the East Indian region. However, as pointed out by Schmidt (1945), such a taxonomic arrangement does not conform with the known facts of marine zoögeography. During the greater part of Tertiary time, straits were open between North and South America, permitting genetic intercourse between tropical Atlantic and East Pacific populations of most marine organisms; whereas the great stretch of open water between Polynesia and the New World has long served to isolate West Pacific populations from their East Pacific allies. Thus one would expect the population occurring on the Pacific coast of America to be more closely related to that of the Atlantic coast than to that found in the West Pacific. The Pacific loggerhead (*Caretta caretta gigas*) is considered to occupy the Pacific coast of tropical America, and also the West Pacific and Indian oceans. Here again the taxonomic arrangement, while possible, seems zoögeographically unsound. The ridleys of the Pacific have been split into two races by Schmidt (1953b), apparently on zoögeographic grounds. By this interpretation, there is a race, the East Pacific ridley (*Lepidochelys olivacea remivaga*), on the tropical west coast of the Americas; and another race, the West Pacific ridley (*L. o. olivacea*), in Asiatic waters. It should be emphasized that the current arrangement of cheloniid turtles, or rather the several different arrangements that have been proposed, have largely been based on reasoning or on zoögeography and not upon the examination of large series of specimens from different areas. There is a further possibility that, in some cases, the open Atlantic serves to isolate the Mediterranean-African population from the West Atlantic one. The confused state of sea turtle taxonomy emphasizes the vast amount of herpetological work remaining to be done in saltwater areas.

The East Pacific green turtle ranges coastally from southern Chile to southern California. Little is known of its habits. Carr (1952) provided most of the available information; also see Brattstrom (1955) and Stebbins (1954). It inhabits bays and island shores, especially where waters of moderate depth cover beds of *Zostera* or kelp. These plants are eaten, and pieces of sponge were found in one stomach.

The West Pacific green turtle is better known, having studied by Banks (1937), Burton (1917), Deraniyagala (1939), Günther (1864), Harris (1931), Hornell (1927), Mawson (1921), Mellen (1925), Moorhouse (1933), Nelson (1921), Raven (1946), and M. A. Smith (1931). It is largely herbivorous, feeding on marine vegetation, although sponges, jelly-fishes, and other invertebrates are sometimes eaten. The young probably are more carnivorous than the adults. The dependence of the adults upon marine pasturage may be the chief factor restricting their geographic occurrence.

The Pacific hawksbill turtle is said to inhabit the waters of the tropical Pacific as far north as Japan; the African coast as far south as Madagascar; and the American coast from Baja California to Peru. A few strays may turn up along the California coast. This race has been considered by Bennett (1843), Carr (1952), Deraniyagala (1939), and Hornell (1927). It inhabits bays, lagoons, and estuaries, usually bordered by mangroves; and also enters brackish creeks and passes. It sometimes occurs in areas where bottom vegetation is lacking. The food includes algae, sea-weed, mangrove leaves and fruits, jelly-fishes, mollusks, and crustaceans. Captive specimens will accept fish readily. The shell and flippers of this turtle are often attacked by barnacles and boring mollusks; this is true to some extent of all the cheloniids, but is particularly the case with the Pacific hawksbill, which appears to be more nearly sedentary than the other sea turtles.

The Pacific loggerhead ranges from southern California to Chile on the American coast, and also inhabits the Indian Ocean, the African coast, and the western Pacific. It has been studied or remarked on by Carr (1952), Ditmars (1910, 1936), Deraniyagala (1933, 1939), Pope (1939), and Stebbins (1954). It is a wanderer, and may be found not only in bays and lagoons, but also in the lower neritic and occasionally in the oceanic zone. It is known to eat crabs, mollusks, oysters, and sea-urchins; thus it appears to be essentially carnivorous like its Atlantic ally. It was but recently found in United States waters (Shaw, 1947). On Clarion Island in the Revillagigedo Archipelago, about 210 miles southwest of the tip of Baja California, a hatchling of the Pacific loggerhead was found in the stomach of a snake, the Clarion Island racer (*Masticophis anthonyi*) (Brattstrom, 1955).

The East Pacific ridley ranges coastally from Baja California to Chile. Its habits have been remarked on by Carr (1948, 1952) and Oliver (1946). It occurs mainly in relatively shallow, protected water. It is more of a bottom dweller than the other cheloniid turtles, which

often float at the surface. Deep water is sometimes entered, however. It appears to be somewhat omnivorous, feeding upon marine invertebrates as well as vegetation. The West Pacific ridley inhabits the tropical West Pacific as far north as Japan; there are also records of ridleys (subspecies not known) off the coast of South and West Africa. The West Pacific ridley has been studied by Deraniyagala (1933, 1939) and Greaves (1933), and appears similar to the East Pacific race in habits and habitat.

The cheloniid turtles have all been valued as food at certain times and places. The green turtle, especially, has been hunted commercially; it is said to be the most important reptile in the world from an economic standpoint. Sea turtle eggs are often eaten by rural coastal peoples; in parts of southern Asia they are collected literally by the million, and form an important item of aboriginal diet. The hawksbill turtle is the source of "tortoise-shell," once used widely in the manufacture of combs, jewelry, etc., and still utilized by Oriental craftsmen in considerable quantity. Many papers have dealt with commercial and economic aspects of the sea turtles; among them are Alexander (1902a, 1902b), Anderson and Power (1948), Babcock (1938), Boeke (1907), Brice (1897), H. H. Brown (1946), Duerden (1901), Engelhardt (1912), Everman and Bean (1896), Gudger (1919), Martínez (1948), Schroeder (1924, 1931), Seale (1911, 1917), Thompson (1947), Tressler (1923), True (1884), and Yonge (1930). Still others are listed and summarized by Ingle and Smith (1949).

Cheloniid turtles are parasitized by a goodly number of organisms, including marine borers, leeches, blood flukes, trematodes, and cestodes; barnacles and other sessile marine organisms grow upon the reptiles' shells and flippers. The parasites and epizoönts of sea turtles have been discussed by Luhman (1935), Nigrelli (1940, 1941, 1942), Nigrelli and Smith (1943), Nilsson-Cantell (1930, 1932), Pilsbry (1910), Pratt (1914), Price (1934, 1939), Richards (1930), and Smith, Coates, and Nigrelli (1941). Still other parasitological papers are cited by Ingle and Smith (1949).

Some additional papers, mostly of a general nature and dealing with some aspect of sea turtle biology, include Agassiz (1888), Babcock (1919), Catesby (1730), Cowan (1938), Deraniyagala (1930a, 1932, 1943), Despott (1914), Grant (1911a, 1911b, 1927), Loveridge (1945), Musgrove and Whitley (1926), H. W.

Parker (1939a, 1939b, 1939c), Roosevelt (1917), Russel (1939), and Schnee (1898).

Numerous papers have dealt with the anatomy, behavior in captivity, conservation, cultivation, distribution, embryology, growth, longevity, physiology and taxonomy of sea turtles. I have not attempted to include these in the present bibliography; a great many of them, classified according to subject, were cited by Ingle and Smith (1949), who discussed sea turtles and the turtle industry of Florida, the Caribbean, the Gulf of Mexico, and the West Indies. Ingle and Smith's paper includes an extensively annotated bibliography of more than 350 titles.

Family DERMOCHELYIDAE.—The Dermochelyidae (also called Dermochelidae) includes but a single species, the leatherback sea turtle (*Dermochelys coriacea*). It is the largest of living turtles, reaching a weight of at least 1,200 to 1,500 pounds. Like the cheloniid turtles, it is marine and possesses marked anatomical specializations for sea life. Its similarity to the cheloniids is a matter of adaptive convergence, for the Dermochelyidae and the Cheloniidae are not closely related. Indeed, the leatherback is sometimes placed in a suborder of its own, the Athecae.

This turtle is found in all the warmer seas. Two races are currently recognized: the Atlantic leatherback (*Dermochelys c. coriacea*) and the Pacific leatherback (*D. c. schlegeli*). The habits of the Atlantic race have been remarked on by Babcock (1931, 1938), F. H. Brown (1863), Caldwell *et al.* (1955a), Carr (1940, 1952, 1954b), Coker (1906b), De Kay (1842), De Sola and Abrams (1933), Ditmars (1910, 1936), Faouzi (1936), Ford (1879), Garman (1883), Gosse (1851), Ingle and Smith (1949), Pope (1939), J. Schmidt (1916) and Sears (1886); those of the Pacific race by Anonymous (1932), Carr (1952), Deraniyagala (1930a, 1936b, 1939), Ditmars (1910, 1936), Kermode (1932), Kloss (1907), Pope (1939), Stebbins (1954), Tweedie (1953) and Van Denburgh (1905).

More than any cheloniid, the leatherback is a species of the open seas, often occurring at vast distances from land. Nevertheless, at rare intervals it wanders into bays, or even ascends rivers for short distances. The Atlantic leatherback inhabits the Gulf of Mexico, the Caribbean, the Atlantic, and the Mediterranean, ranging from Nova Scotia to Argentina and from the British Isles to the southern tip of Africa. A century ago it probably nested rather commonly on South Florida beaches; but within recent times there have been but three

records of nesting in this state. One of these was near Flagler Beach (Allen and Neill *in* Carr, 1952), a second at Miami Beach (Allen and Neill, 1957), and a third at Hutchinson's Island in Martin County (Caldwell *et al.*, 1955a). The Pacific loggerhead inhabits the Indian and Pacific Oceans, from Japan to southern Australia and southern Africa, and from British Columbia to Chile and New Zealand.

Nothing much has been recorded concerning the feeding habits of either race. Apparently the species is omnivorous, known food items including jelly-fishes, prawns, fishes, and blue-green algae. The leatherback has never been of any great economic importance. An oil derived from the skin and shell has been employed as varnish; the eggs are eaten whenever found; the turtles themselves are relished in some areas but abjured in others. The flesh of the leatherback is often reputed to be poisonous, although the observations of Lowe and Norris (1955b) and Carr (1952) suggest otherwise. It appears likely that leatherbacks (as well as loggerheads and perhaps other cheloniids) once in a while feed upon something that renders the flesh temporarily poisonous.

The leatherback seems virtually immune from barnacle attack, perhaps because it is covered with an oily skin. According to Ingle and Smith (1949), only one endoparasite, a species of trematode, has been reported from this reptile. Certain fishes (*Naucrates ductor* and *Leptechineis naucrates*), equipped with a dorsal suction disk, often attach themselves to the under side of the leatherback's carapace in the posterior region. The latter fish may feed upon the turtle's feces.

CROCODILIANS

Family CROCODYLIDAE.—The Order Crocodilia includes those reptiles commonly known as crocodiles, gavials, caimans, and alligators. All of them are large and essentially carnivorous; they live a semi-aquatic life, usually about fresh water. The crocodiles, of which about 15 species are known, comprise the family Crocodylidae.

The estuarine crocodile (*Crocodylus porosus*), as its name implies, is of frequent occurrence in brackish water. It ranges from South China and the Philippines to northern Australia, inhabiting the lower reaches of streams, estuaries, brackish swampland, mangrove swamp, and the open sea (Barbour, 1928b; Boulenger, 1912; Broughton, 1936; De Rooij, 1915; De Sola, 1933; Loveridge, 1945; Mertens, 1927, 1930, 1934; Tweedie, 1949). According to Deraniyagala

(1939), it is commonly associated with mangroves and with a flag (*Lagenandra toxicaria*) from which it constructs its nests. It sometimes occurs along the upper reaches of streams and in freshwater swamps, but in general may be considered a brackish water species. Two specimens were thought to have reached Cocos-Keeling Atoll by swimming 600 miles (Wood-Jones, 1909), and records of the species from Palau and the Fijis may be based on wandering individuals rather than populations (Strauch, 1866). I saw a large adult, badly wounded by natives' spears, wallowing in the surf at Port Moresby, Papua; and many small examples were observed in the catch of Chinese and Malayan fishermen operating off the coast of Merauke, Dutch New Guinea. This is the largest of all crocodilians, and the most frequent predator on man (Cochran, 1944). It unquestionably takes a toll of human life about the Australasian waters. (On one occasion it reversed the usual process by attempting to collect a biologist; see Loveridge, 1944.) However, where firearms are available to the local residents, it is hunted extensively for its hide; and the hatchlings are frequently mounted for the souvenir traffic.

The Siamese crocodile (*Crocodylus siamensis*) is "equally at home in both fresh and salt-water" (De Sola, 1933, p. 17). The Ceylonese marsh crocodile (*C. palustris kimbula*) commonly invades salt water, although its Indian ally (*C. p. palustris*) but rarely does so (Deraniyagala, 1930b, 1939; M. Smith, 1931).

The Nile crocodile (*Crocodylus niloticus*) of Africa has been found on the beach near the mouth of the Congo River; one specimen took to sea when frightened, and another was caught in the sea (Hesse, 1889). The usual habitat is fresh water. The sharp-nosed African crocodile (*C. cataphractus*) was seen daily at low tide about the mangrove zone of several river mouths in the Cameroons (Sjöstedt, 1897); it also occurs in fresh water. Attenborough (1955) figured the capture of a crocodile in a mangrove swamp of Sierra Leone; it was not identified as to species, but probably was *C. cataphractus*. The West African rough-backed crocodile (*Osteolaemus tetraspis*) is "often found in salt or brackish water where its upturned snout is useful in keeping its head above choppy waves," according to De Sola (1933, p. 17).

The American crocodile (*Crocodylus a. acutus*) occurs in South Florida, as well as on many islands of the West Indies, the Caribbean coast from Yucatan to Colombia, and the Pacific coast from Sinaloa, Mexico, to Ecuador. Two races have been recognized: *C. a. lewyanus*

in Colombia and Venezuela, and *C. a. acutus* elsewhere. The habits and distribution of the American crocodile in Florida have been discussed by Allen and Neill (1952a, 1952c) and Moore (1953a). At one time it was found from the head of the Indian River on the East Coast, and probably from the Ten Thousand Islands on the West Coast, southward through the Keys (Barbour, 1923). The activities of commercial hide hunters soon reduced its range, however. Today it is confined largely to the islands in Florida Bay; a few specimens persist in Biscayne Bay and along the Florida Keys. Moore (1953a) could find none in the Ten Thousand Islands region at present, nor did he observe any at Cape Sable. This reptile, in Florida, is now restricted mainly to salt water, especially shallow water in the vicinity of islands and mangrove swamps. It moves upstream with the rising salinity toward the end of the dry season. It requires nearby sandy beaches, in which the females dig their nests. In captivity it does well in fresh water, living for years in this medium. Elsewhere than in Florida, this crocodile sometimes occurs in fresh water and at fairly high altitudes; its restriction to salt or brackish water in Florida may result from inability to compete with the American alligator (*Alligator mississippiensis*). For further observations on the crocodile in Florida, see E. R. Allen (1938a), R. P. Allen (1947), Allen and Neill (1949), Barbour (1922, 1945), Bean (1953), Carr (1940), Cory (1896), J. H. Davis (1943), Dickinson (1953), Dimock and Dimock (1918), Hornaday (1875), Maynard (1876), Moore (1953b), and Wyman (1869, 1870).

Underwood (1950) supplied information on the American crocodile in Jamaica, and recounted an interesting experiment. He kept part of a brood of crocodiles in salt water, the remainder in fresh. The former died in a few days, while the latter survived. On the other hand, Grant (1940a), who also discussed the habits of the species in Jamaica, reported that young crocodiles would not thrive in fresh water. He found nests on the beach, a few feet from the ocean but a mile from any fresh or merely brackish water. C. B. Lewis (1942) likewise reported on the habits of the species in Jamaica, where it seems to be characteristic of mangrove swamp. Barbour and Ramsden (1919) thought it was confined, in Cuba, to saltwater areas such as mangrove swamp and estuaries; however, E. Ross Allen and I found it to be abundant well up the Rio Encantado in fresh waters of the Ciénaga de Zapata. Noble (1923) found a crocodile in Lake Enriquillo, a salty "dead sea" bordered by salt flats, in the Dominican

Republic. The salinity of this lake is 50 per cent greater than that of sea water, and no fishes live in it. The crocodile was not identified as to species, but *Crocodylus acutus* is the only one to occur on the island. Peters (1954) discovered the American crocodile in lagoons along the beach of Michoacán, Mexico.

The Cuban crocodile (*Crocodylus rhombifer*) is confined to Cuba and the Isle of Pines. In general, it appears to be ecologically separated from the American crocodile, being freshwater and palustrine while the latter is saltwater and fluviatile. Gundlach (1880) long ago observed that the two were not found together. Apparently, however, *C. rhombifer* will invade the salt water where *C. acutus* is lacking; for on the eastern shore of the Ensenada de Cochinos, where *C. acutus* had never been observed, Barbour and Ramsden (1919) found *C. rhombifer* common about beaches and mangrove swamps.

A specimen of the Orinoco crocodile (*Crocodylus intermedius*) once came ashore in Grenada (Underwood, 1954). Presumably it swam to the island from the mouth of the Orinoco (to which river system it is normally confined).

Family ALLIGATORIDAE.—This family includes the alligators (two species) and the caimans (six species).

The American alligator (*Alligator mississippiensis*), common in Florida, inhabits freshwater streams, lakes, ponds, and swamps of the Southeastern United States. In addition, it "thrives in marshes where the water is subject to tidal influence but is still fresh, and to a lesser extent is found in brackish marshes"; it was also observed in an actual salt marsh of South Carolina (Allen and Neill, 1949, p. 111). Three alligators, collected in salt water at Key West, Florida, were "unusually fat, healthy specimens of a bright color" (Allen and Slatten, 1945, p. 25). Along the coast of extreme southwestern Florida, alligators and crocodiles are sometimes found in the same area (Allen and Neill, 1949, 1952e). Carr (1940) remarked on the occurrence of the alligator in brackish and salt waters of Florida, and listed it as "frequent" in both mangrove swamp and salt marsh. V. J. Allen and I saw a specimen in salt water at Cedar Keys, Florida. Engels (1952) reported the species from a slightly brackish pond on Ocracoke Island, North Carolina. Obrecht (1946) found it in brackish streams and coastal marshes near Myrtle Beach, South Carolina. He observed several old nests in tidal marshes, suggesting that the alligators were not mere visitors from freshwater habitats. M. J. Allen (1932) saw alligators in coastal marshes and in the bay at Biloxi, Mississippi; a

nest with 25 eggs was found on the bay shore about 20 feet from a brackish marsh. Mc Ilhenny (1935) remarked on the presence of the alligator in salt water. In tidal marshes of Louisiana, the alligator was found to eat large quantities of crabs, crayfishes and shrimp, as well as a few mullet, silversides, menhaden, gars and other fishes (Kellogg, 1929). Presumably the marshes were brackish. James R. Dixon (personal communication) observed the species in the brackish drainage from Lake Austin, Texas.

The Chinese alligator (*Alligator sinensis*) is confined to the drainage of the Yangtze River. It has not been authentically reported in salt water, but there is a local tradition of its presence about an inlet of the sea near Kwangzefu in Kwangtung Province (Barbour, 1922). This may, of course, be no more than a legend.

The brown caiman (*Caiman sclerops fuscus*), found from southern Mexico to Colombia, inhabits brackish marshes as well as freshwater ones. According to Fred Medem (*in* Pope, 1955), the reptile was found in brackish water at the mouth of the Rio Magdalena, Colombia; stomach contents in this area included mollusks and crabs.

LIZARDS

Family IGUANIDAE.—This family is confined to the New World, with the exception of two genera in Madagascar and one in Polynesia. There is great variety of size, form, and habitat among iguanids. One species, the marine iguana (*Amblyrhynchus cristatus*), has often been referred to as the only marine lizard in existence, although this is not precisely the case. It is confined to certain islands of the Galapagos group, where its remarkable habits have been studied by Beebe (1924), Darwin (1884), Schmidt (1935), Slevin (1935), and Van Denburgh and Slevin (1913). It dwells along every type of shore in the Galapagos, but is most characteristic of the shelving plates of "glassy lava" around the edges of the islands. It is seldom seen more than 50 feet inland. At one time enormous aggregations of these lizards were found; a photograph made early in the 1900's by R. J. Beck portrayed acres of lava all but concealed by droves of marine iguanas. Such numbers were made possible by the absence of predators and the presence of an abundant food supply. The lizards feed upon a glutinous marine alga which grows about the islands' shores. At low tide the reptiles enter the surf where the algal growth is abundant, and anchor themselves firmly to rocks by means of their powerful legs and heavy, recurved claws. Sometimes they are inundat-

ed to a depth of several feet by surging tide. They swim well, by undulations of the body and the flattened tail; nevertheless they are reluctant to enter the water when disturbed. If thrown into the surf, they dive to the bottom and walk shoreward by clinging to submerged rocks. Nesting holes are dug in boulder-strewn, sandy areas. For additional observations see Barbour (1926), Heller (1903), Loveridge (1945), and Mertens (1927, 1934).

On various islands of the West Indies are found the rock iguanas (genus *Cyclura*). In many ways they are reminiscent of the marine iguana, but are more generalized in anatomy and habits. They usually dwell about rocky or sandy shores. Species of the larger islands, such as *C. macleayi* of Cuba, once ranged well into the interior; but the activities of man have nearly or quite exterminated many populations, and the lizards' last stronghold generally is some remote coastal area or outlying key. According to Buide (1951), the Cuban species may live in an area where there is no fresh water for drinking, not even pits or hollows of rainwater. Buide was told by fishermen that the rock iguana had been seen swimming from key to key, crossing water gaps of more than 200 yards. E. Ross Allen and I saw a dead specimen which drifted up on the shore near Batabanó; in this area, and at Punta Brava, we found these lizards to inhabit crab burrows. They are often seen basking on inclined trunks and branches of the button mangrove (*Conocarpus*), and the limbs of the red mangrove (*Rhizophora*), according to C. B. Lewis (1944). The habits of the Cuban species on Cayo de la Piedra have been discussed by L. H. Saxe (*in* Sutcliffe, 1952). On this key it exists mostly in supratidal situations, feeding on prickly-pears (*Opuntia*) and crabs. Wild specimens of the Little Cayman Islands population (*C. macleayi caymanensis*) feed upon leaves and flowers of goat's-foot (*Ipomoea pes-caprae*) and other plants characteristic of coastal dunes (C. B. Lewis *in* Grant, 1940b). The population on Anegada Island (*C. pinguis*) was found to eat sea-grape (*Coccoloba*) leaves, cactus (*Opuntia*) fruit, and whole wild nutmegs (Grant, 1937).

Most impressive of the rock iguanas is the rhinoceros iguana (*Cyclura cornuta*) of the Hispaniolan region. On Petite Gonave it feeds upon "harsh fruits and shore crabs" (Eyerdam, 1954). Noble (1923) studied the habits of this reptile about Lake Enriquillo, a briny "dead sea" bordered by salt plains, in the Dominican Republic. The salinity of the lake is said to be 50 per cent greater than that of sea water, and no fish live in it. The huge lizards dwell in tunnels of coral limestone

about the lake. At nearby Lake Saumâtre, likewise saline, one of these lizards ran into the water when pursued, and remained submerged for nearly five minutes. On a sandy island in Lake Enriquillo, Noble found another species of rock iguana (*C. ricordi*). These reptiles dug holes in the flat, salt-encrusted playas.

The large lizards of the genus *Ctenosaura* are also called rock iguanas; they are related to *Cyclura* but inhabit Mexico and Central America. The spiny-tailed rock iguana (*Ctenosaura acanthura*) is found on sandy beaches of Mexico (J. W. Bailey, 1928); a species of southern Baja California (*C. hemilopha*) sometimes eats crabs (Van Denburgh, 1922); a race of this species (*C. h. conspicuosa*) has been found on Isla Lobos, a tiny, cactus-covered rock-like island off the coast of Sonora, Mexico (Lowe and Norris, 1955a); a third species (*C. similis*) is found on sandy beaches of Panama, especially those with rocky outcroppings, and rarely ventures more than 200 yards inland (J. W. Bailey, 1928). A. M. Bailey (1941, p. 347) figured a lizard, evidently a *Ctenosaura*, on Isabela Island off the coast of Mexico. He called it a "marine iguana" and described its method of swimming in the sea.

The true iguana (*Iguana iguana*) is widespread in the New World tropics from Mexico to South America. Although arboreal, it swims well. It is often found over water, into which it dives when molested. Mertens (1927) thought it ventured only into fresh water. However, Grant (1932b) was told by residents of the Virgin Islands that the iguanas of that area, when disturbed, would dive into the sea and cling to rocks. On Water Island, near St. Thomas, Grant (1937) found iguanas about brackish lagoons, into which they would leap and swim away. Similar observations were made by Grant on St. Croix, where he also saw iguana tracks on the beach.

Turning to the smaller iguanids, it is not surprising to find that some of the arenicolous ones venture onto beaches, saxicolous ones onto coastal rocky outcroppings, and arboreal ones into supratidal vegetation. The zebra-tail lizard (*Callisaurus draconoides*), a sand dweller, was found on a spit of land projecting into the Bahía de los Angeles, Baja California. "Tidal wrack on the surrounding beach attracted these lizards, many of whom foraged over the beach up to 45 feet from cover and to within 5 feet of the water's edge." The lizards fed upon small beach insects and crustaceans. They basked upon fish carcasses, gastropod and pelecypod shells, and other beach debris. When disturbed, they ran for cover in thickets of salt bush (Tevis.

1944, p. 8). Tevis also noted the banded rock lizard (*Petrosaurus mearnsi*), the small-scaled lizard (*Urosaurus microscutatus*), and the granite spiny lizard (*Sceloporus orcutti*) on lava cliffs along Coyote Bay, Baja California; and the side-blotched lizard (*Uta stansburiana*) on beach dunes at Bahía de los Angeles. Hurter (1912) found the side-blotched lizard to be common on cliffs along the coast at Laguna Beach, California, practically within reach of salt spray. According to Stebbins (1954), this species, although common on beaches, rarely invades the strand. *Urosaurus auriculatus*, of Socorro Island in the Revillagigedo Archipelago, was found under debris on beaches and in rocky or grassy supratidal areas just behind the beaches, tidepools, and sea cliffs (Brattstrom, 1955; Slevin, 1926). *U. clarionensis*, of Clarion Island in the same archipelago, may also be found in dry supratidal situations (Brattstrom, 1955). I have observed the desert iguana (*Dipsosaurus dorsalis*) on dunes beside the Salton Sea, a man-made salt lake in southern California.

E. Ross Allen and I saw many crested lizards (*Leiocephalus carinatus*) about the sandy, rock-strewn shores of Morro Castle island, just off Havana, Cuba. According to Barbour and Ramsden (1919), this species is characteristic of coastal stretches, especially rocky ones, being associated with supratidal vegetation. Schwartz and Ogren (1956) observed it on rocks and driftwood at the foot of sea cliffs in Cuba. Schmidt (1930) stated that the lava lizards (genus *Tropidurus*) "which would elsewhere be insectivorous," are perforce crab-eaters on Narborough Island in the Galapagos group.

The familiar Carolina anole or "chameleon" (*Anolis c. carolinensis*), an arboreal lizard of the southeastern United States, sometimes occurs in supratidal vegetation. Carr (1940) listed it as "frequent" in Florida mangrove swamp. I have often found it in salt marsh, also. Corrington (1927) observed it on fences and walls fronting beaches at Biloxi, Mississippi. Along the southwest coast of Florida, from Fort Myers at least to Everglades City, there occurs an unnamed race of this anole, characterized by (among other things) a green throat-fan instead of a pink or red one. Although ranging a short distance inland, it is characteristic of supratidal vegetation, and its diagnostic features may represent adaptations to life therein. The Key West anole (*Anolis sagrei stejnegeri*) was first discovered running along the railing of a bridge across a saltwater ditch, on the island to which it is confined (Barbour, 1931). I have found it on trunks of palm trees in close proximity to the beach. A distinctive anole (*Mariguana agassizi*)

is confined to Malpelo Island, a barren basaltic rock about 250 miles off the Colombian coast. The island supports no trees, shrubs or herbs; and the lizards are found running about on rocks overhanging the sea (Slevin, 1928; Stejneger, 1900). The original specimens were collected from a boat (Barbour, 1930). Mertens (1952b) found an anole, species not named, and a spiny lizard (*Sceloporus variabilis olloporus*) about fallen logs and tree roots growing near high tide mark on a beach at Punta Gorda, El Salvador.

A Cuban lizard, *Norops ophiolepis*, is closely related to the anoles, but dwells on the ground and in low grass. I have found specimens sleeping at night on stems of saltmarsh vegetation near Havana. The basilisks (genus *Basiliscus*), likewise related to anoles, are arboreal lizards of the Neotropics. They are often found in bushes near the water, into which they will leap or dash when pursued; and possess the ability to "skitter" over the surface without sinking. According to Mertens (1927), they frequent fresh water only; but one species (*B. vittatus*) was recently found along the littoral zone in Michoacán, Mexico (Peters, 1954, p. 12). There it was confined to thick undergrowth surrounding brackish lagoons, its "favorite haunt being the root tangles of mangrove." Another species (*B. basiliscus*) is common about "streams and shores" of Ruatan Island, off the coast of Honduras (Barbour, 1928a).

A "horned toad" (*Phrynosoma douglassi ornatus*) inhabits salt flats around Great Salt Lake, Utah, and its color matches the substratum (Woodbury, 1952).

The Madagascan *Hoplurus quadrimaculatus*, one of the few Old World iguanids, has been found in the littoral zone as well as in the interior (Angel, 1950).

FAMILY ANGUIDAE.—The family Anguidae (or Anguinidae) includes a variety of lizards, among which the "glass-snakes" (genus *Ophisaurus*) and alligator lizards (genus *Gerrhonotus*) are perhaps the best known. The primitive anguid lizards of the genus *Diploglossus* inhabit South and Central America as well as portions of the West Indies. The common name of "galliwasp," used for a Jamaican species, is sometimes applied to the entire genus. One species (variously known as *D. millepunctatus* or *Celestus hancocki*) occurs on isolated Malpelo Island, and appears to be thoroughly adapted to life along the sea's edge. As mentioned previously, Malpelo is little more than a barren basaltic rock without higher plants. The lizards are found about the rocky shores. They have no hesitancy in entering the water,

and, when pursued, will take refuge in tide pools, submerging except for their heads. Stomach contents of nine specimens included only crab fragments and the feathers of sea birds (Slevin, 1928; Mertens, 1930). A Jamaican species (*D. occiduus*) was found under piles of coconuts, along with land crabs in what may have been a supratidal situation near Montego Bay (Grant, 1939). It sometimes eats marine crabs (Ahrenfeldt, 1954).

The anguid genus *Ophisaurus* includes both New and Old World forms, all of them essentially limbless and of serpentine habit. The United States species, three in number, are popularly called "glass-snakes," although herpetologists prefer the name "glass-lizard." The habits of the island glass-lizard (*O. compressus*) have been discussed by Neill (1948; and in McConkey, 1954) and by Allen and Neill (1952b). It inhabits coasts and offshore islands of South Carolina, Georgia, and Florida, as well as the vicinity of "scrub" patches in the interior of Florida. Rosemary scrub (*Pinus clausa* and *Ceratiola ericoides* association) is generally considered to be the first timber stage following cessation of activity in coastal dunes, and the scrub patches of interior Florida are thought to indicate the position of Pleistocene (or late Pliocene) islands (Carr, 1940; Neill, 1951a). The distribution of *O. compressus* favors the theory. This lizard is often abundant on beaches, where it prowls about the tidal wrack zone. It is particularly common about thick piles of palmetto leaves cast up by the waves. I have frequently lifted a handful of dead fronds and noted three or four of these lizards and dozens of fiddler crabs scurrying off in all directions. It also occurs in thick stands of beach grasses, such as sea-oats (*Uniola*). Several herpetologists have heard the story that the island glass-lizard swims in the ocean and feeds on fish. The origin of this tale I do not know. The type specimen, which for years remained unique, was flattened in a vertical plane, as though for swimming; and this circumstance, coupled with the insular distribution, may have given rise to unwarranted assumptions. Actually, the compression of the body was an artifact of preservation. It is interesting to note, however, that Engels (1952) found a glass-lizard swimming in a slightly brackish pond on the Shackleford Banks, North Carolina. Engels referred the specimen to *O. ventralis*, but I should not be surprised to find that it was *O. compressus*. Obrecht's (1946) record of *O. ventralis* in a dune-grass section of Myrtle Beach State Park, South Carolina, and T. H. Lewis' (1946) record of *O. ventralis* from a pile of driftwood on Smith Island, North Carolina, may also

be based on *O. compressus*. Immediately after the hurricane of 1950. E. Ross Allen and I found dead examples of both species on the causeway leading to Cedar Key, Levy County, Florida. I found the western slender glass-lizard (*O. a. attenuatus*) in coastal marsh near Sabine Pass, Texas. On Soltu Island in the Adriatic, an Old World glass-lizard (*O. apodus*) was observed to flee into the ocean and hide beneath a rocky overhang (Mertens, 1927).

Another Old World anguid, the "slow-worm" (*Anguis fragilis*), is common on the southwest coast of England, often near the sea and in places drenched by salt spray during storms (M. Smith, 1951).

Family SCINCIDAE.—The cosmopolitan family Scincidae includes a vast array of lizards, most of them rather small. Some of the species are burrowers, in the soil or under ground litter; others dwell about logs, stumps, tree trunks, or rocky outcroppings. The scincid subfamily Lygosominae (as defined by Mittleman, 1952) includes about 600 species scattered over 33 genera. Lygosomine skinks are especially abundant on islands of the Southwest Pacific. Many of the species seem especially fitted for overseas dispersal, and have extended their distribution to various farflung islands. Thus a snake-eyed skink (*Cryptoblepharus boutoni*) ranges from the Bonins to Australia and thence eastward across the Pacific to islands off the coast of Peru and Ecuador; and the blue-tailed emo (*Emoia cyanura*) ranges from Borneo to the New Guinean region and thence eastward to Clipperton Island, about 700 miles off the west coast of Mexico. It is not surprising to find various lygosomine skinks about saltwater habitats. The snake-eyed skink has been reported from beaches, and from rocky or coralline cliffs within reach of sea spray (Loveridge, 1945; Neill, 1946). According to the former author, lizards of this species often feed upon sandhoppers, sea slaters, and other small marine life. On Owi Island, off the north coast of New Guinea, I found a green skink (*Dasia smaragdina perviridis*) on the trunks of coconut palms in reach of salt spray. Martens (1876) and Mertens (1927) reported an Ambonese skink (*Leiolopisma fuscum*) about rocks at the edge of the sea; a related species (*L. noctua*) of Polynesia was found in a beached native canoe and under trash of the sea beach (Schmidt, 1930). On Eniwetok, the latter inhabits areas of herbaceous vegetation along beach dunes, where its toes are frequently nipped off by a species of crab (Oliver and Shaw, 1953).

One of the emos (*Emoia atrocistatum*) is confined to beach habitats in the Bismarck Archipelago. Its habits have been described

by Hediger (1934), Kopstein (1926), Mertens (1927, 1934) and Sworder (1924, 1925). It enters the sea without hesitation, and in fact takes refuge in the sea when pursued. It occurs on offshore reefs, which it may reach by swimming. Its food includes mainly small beach crustaceans; small marine fishes are also eaten. According to Mertens (1934), a related species (*E. nigra*) is of similar habits; but Hediger (*op. cit.*) believed that records of *E. nigra* about salt water were based on misidentified specimens of *E. atrocostatum*. Another emo (*E. caeruleocauda reimschiisseli*) occurs about the coral ledges bordering Morotai Island in the Moluccas (Tanner, 1950). On this island I once found several of these skinks under tarpaulins spread out on the beach.

A diminutive skink, *Ablepharus wahlbergi*, was taken in abundance at the roots of stumps in sandy soil, about 100 yards from the sea in Mozambique, Portuguese East Africa (Barbour and Loveridge, 1928).

The ground skink (*Lygosoma laterale*) inhabits the southeastern United States, occurring through Florida. It dwells beneath leaf litter and other ground debris, being largely independent of the major habitat boundaries. It is sometimes found beneath logs and leafy debris in dry supratidal situations, but seems to avoid spots that are actually damp with spray.

A few skinks of other subfamilies have been noted in saltwater habitats, although seldom with any frequency. The red-tailed skink (*Eumeces e. egregius*) of South Florida has been found around "piles of rock, debris, and wave-washed wrack on the Florida Keys" (Carr, 1940, p. 75). The Florida five-lined skink (*E. inexpectatus*) occurs in supratidal situations, including the border of mangrove swamp; it thrives on small islands and keys about the Florida coast (Carr, 1940; H. M. Smith, 1946), as well as in the interior of the state. A mabuya skink (*Mabuya atlantica*), of Fernando Noronha Island 375 miles off the Brazilian coast, occurs under rocks of the sea beach as well as of the interior (Finley, 1945). Another mabuya (*M. elegans*), found in Madagascar, inhabits the littoral zone as well as the interior (Angel, 1950). Two skinks (*Chalcides ocellatus* and *C. tridactylus*) were found by Bellairs and Shute (1954) very near the beach, in what might be a supratidal zone, near Bougie, Algeria. The former was also found under stones near the beach at Bushire, Iran (Schmidt, 1955). Blanford's skink (*Ophiomorus blanfordi*) of Baluchistan, discovered in 1879, was not seen again until Shockley (1949) described its habitat. It dwells in ground burrows amid clumps of grass growing

above high tide mark along the coast. The African *Scelotes aeneus* was first discovered about the roots of stumps in a supratidal zone at Lumbo, Mozambique, Portuguese East Africa (Barbour and Loveridge, 1928).

Family AGAMIDAE.—The family Agamidae is an Old World one. In their adaptive radiation and concomitant modifications the agamid genera often parallel those of the essentially New World Iguanidae. The sail-tailed lizards (genus *Hydrosaurus*), of various Western Pacific islands, are remarkably modified for semi-aquatic existence. The tail and posterior portion of the body bear a high, sail-like crest, which functions like a sculling oar as the reptile swims. These very large lizards are customarily found on tree branches over water, into which they dive when alarmed. Specimens collected by me on Luzon, Philippine Islands, smelled strongly of fish, upon which I presume they prey. I found the Philippine species only in fresh water. However, Taylor (1928) suggested that these lizards swam from island to island. A medium-sized agamid lizard (*Physignathus temporalis*) was observed by me in mangrove swamp at Port Moresby, Papua. It climbed among the mangrove branches, and sometimes when pursued would dive into tide pools. Other specimens darted about over the sea-wet ground and sought refuge in crab holes. The same species was observed about freshwater ponds farther inland. A larger species, the so-called water dragon (*P. leseueri*) was seen by me in bushes overhanging the mouth of a small stream near Sydney, New South Wales, Australia. On Morotai Island in the Moluccas I found a small, arboreal agamid (*Calotes cristatellus moluccanus*) to be common on brush growing along coral ridges at the edge of the sea, and also on piles of cut brush thrown onto the beach.

Family VARANIDAE.—The monitor lizards, family Varanidae, are confined to the Old World. Most of them are large; and one, the Komodo dragon (*Varanus komodoensis*) is the largest extant lizard, reaching a weight of 250 pounds or more. Several of the monitors are excellent swimmers. The common water-monitor (*V. salvator*) is found in parts of southern Asia and Indonesia. Loveridge (1945, pp. 61-62) attributed its extensive distribution to its prowess as a swimmer. Its long, vertically flattened tail and valvular nostrils are probably adaptations to a semi-aquatic existence. Water-monitors are characteristic of coastal canals and river deltas, and have been seen swimming far out at sea (Cochran, 1944). M. A. Smith (1932) considered these lizards to be equally at home in fresh water or salt, and

stated that coastal specimens hunted crustaceans and mollusks along the shore when the tide was out. He had seen these lizards in the Gulf of Siam, swimming between islands that were well over a mile apart. Taylor (1928) doubtless had this species in mind when he suggested that monitors swam from island to island in the Philippines. At the mouth of the Agno River on Luzon, Philippine Islands, I observed these monitors on tree trunks overhanging the water, into which they dived when approached. They fed upon chickens which were penned nearby. For additional remarks on this species, see H. C. Smith (1931).

The Indian water-monitor (*Varanus indicus*) also invades salt water (Mertens, 1927). Specimens were found in mangrove swamp on Yap Island in the Carolines (Fisher, 1948). An example from Morotai Island, in the Moluccas, had eaten a crab (Tanner, 1950). Dumeril's monitor (*V. dumerili*) is another member of the water-monitor group, inhabiting the Borneo-Java-Sumatra area. According to Loveridge (1945), it inhabits mangrove swamp and dense evergreen forest near the coast. When pursued by dogs, it has been known to dash across the beach and take refuge in the sea. M. A. Smith (1932) thought that these monitors swam from island to island in the Mergui Archipelago. Raven (1946) found monitor lizards to be common on the beach of an islet 30 miles off the Bornean coast. Here the lizards were seeking out nests of the green turtle (*Chelonia mydas*) in order to devour the eggs. The monitors were not identified as to species, but may have been *V. dumerili*. A common African monitor (*V. niloticus*) is also semiaquatic at times, and can remain submerged for an hour (M. A. Smith, 1932). In Natal, Cowles (1930) found it only near water, into which it would leap when disturbed. Cowles did not actually report specimens in salt water, but mentioned that stomach contents included crabs.

The Komodo dragon is confined to a group of islands in the Lesser Sundas. Essentially a terrestrial and inland species, it feeds largely upon deer and wild hogs, and perhaps even wild horses, as well as carrion, birds, and birds' eggs. However, on Padar Island these giant lizards frequent the beaches, where they dig up sea turtle nests; Burden (1928) considered turtle eggs to be the main food at this locality. Burden found the monitors to be moderately proficient swimmers. Some captive specimens, released on the beach, dashed into the sea. Two of them swam submerged for two minutes, covering 70 yards in this time; then they swam parallel to the beach for about a mile, and

returned to land. Broughton (1936) observed this species on the beach at Komodo. Tracks of the lizards, and also of crocodiles (doubtless *Crocodylus porosus*), were seen in the sand; and on one occasion a snare, set for the monitors, caught a crocodile instead.

Family LACERTIDAE.—The family Lacertidae is an Old World one. Its members are often referred to as “typical lizards.” Several small lizards of the genus *Lacerta* are abundant in the Mediterranean region. Although not considered aquatic, some of them are not averse to entering water. One species, the common wall lizard (*L. muralis*), was found by Billiard (1914) on the coast, where it entered the sea and fed on small crabs and amphipods. Mertens (1927) also remarked on the occurrence of this species in saltwater habitats. In England the viviparous lizard (*L. vivipara*) is sometimes found on coastal dunes and on the seashore “almost within splash of the waves” (M. A. Smith, 1951, p. 194). On Okinawa, in the Ryukyus, I found a green arboreal lacertid (*Takydromus smaragdinus*) in vines growing over shrubs at the edge of the sea. The spiny-toed lizard (*Acanthodactylus c. cantoris*) of India inhabits coastal dunes, where it seeks refuge in burrows beneath clumps of supratidal vegetation (Shockley, 1949; Mertens, 1954). Bellairs and Shute (1954) found a small lacertid (*A. vulgaris*) in the intertidal and supratidal zone near Bougie, Algeria, and a few specimens of another lacertid (*Psammodromus algirus*) near the beach in the same area.

Family TEIIDAE.—The New World family Teiidae includes a number of species, such as the familiar six-lined racerunner (*Cnemidophorus sexlineatus*), which dwell about sandy places. It is not surprising to find some of these species in the dry supratidal zone or even on the beach at low tide. The racerunner was found on the beach and in dune thickets at Ocracoke Island, North Carolina (Engels, 1942). It was observed about dunes on the Shackleford Banks, North Carolina, where it entered burrows of the ghost crab when pursued (Engels, 1952). I saw many specimens on the beach and about tidal wrack at Green Point, Franklin County, Florida. A Mexican racerunner (*C. deppei lineatissimus*) was characteristic of the littoral region and adjoining thorn forest in Michoacán (Peters, 1954). A West Indian species (*Ameiva polops*) was found on the beach at Green Cay in the Virgin Islands. At this locality the food of the lizard consisted of semiaquatic amphipods, probably caught about beached seaweed (Beatty in Grant, 1937). E. Ross Allen and I ob-

served a Cuban whiptail (*A. auberi*) about sandy, rock-strewn shores of Morro Castle Island near Havana. Barbour and Ramsden (1919) considered this species especially characteristic of sandy beaches.

A remarkable teiid is the caiman lizard (*Dracaena guianensis*), found along the coasts of the Guianas and northern Brazil. It is large, with powerful jaws and molar-like crushing teeth. It feeds exclusively upon snails and clams. According to Conant (1955), its habitat is mangrove swamp, and so its molluscan prey must consist of brackish water species.

Family ANNIELLIDAE.—The anniellids are restricted to California and Baja California. The two known species, both of the genus *Anniella*, are called "footless lizards". They lack external evidence of limbs, and are of serpentine habitus. The silvery footless lizard (*A. p. pulchra*) was found by Coe and Kunkel (1906) about sand dunes of the seashore, where it occurred beneath low bushes and under driftwood. Burt (1931) thought it characteristic of moist, sandy soil, and quoted L. M. Klauber to the effect that it was "quite common along the beach where the sand must be decidedly salt". Klauber (1932) pointed out that it also occurred in the desert, and gave the range of a subspecies, the black footless lizard (*A. p. nigra*), as "the shore line from Monterey to San Luis Obispo". L. H. Cook (*in* Klauber, 1939) reported *A. p. pulchra* in sand under boards and rubbish on beaches, and Zweifel (1952) found tracks of this reptile in "sea caves hundreds of feet above the water". Fisher* (1930) discovered *A. p. nigra* on a rocky islet, subject to sea spray throughout, 200 feet off the mainland in Pacific Grove, California. Stebbins (1954) remarked that the range of the species was markedly discontinuous except perhaps along the beach. At Coronado Beach, California, the species was common under sand-verbenas on dunes above high tide mark (Klauber, 1940). The only other member of the genus, *Anniella geronimensis* of Baja California, also inhabits sandy areas, including beaches, being found beneath such plants as *Encelia farinosa* and *Franseria bipinnatifida* (C. E. Shaw, 1953).

Family AMPHISBAENIDAE.—Amphisbaenids are mostly worm-like in appearance. External limbs are absent, except in one genus; an ear opening is lacking; the eyes are minute or concealed beneath skin; and the body scales are arranged in rings. One African species (*Trogonophis weigmanni*) was found beneath stones on various

*This article was erroneously attributed to M. E. Musgrove when originally printed.

beaches of Algeria (Bellairs and Shute, 1954); it may be confined to this habitat.

Family GEKKONIDAE.—The family Gekkonidae is largely confined to tropical and subtropical regions. Most of its members, commonly called geckoes, are small, nocturnal or crepuscular, and secretive lizards which feed upon insects. Some of the geckoes dwell on and under rocks, a great many about tree trunks and beneath rotting bark, and others under ground litter or among epiphytic growths. Several species, the so-called “house” or domestic geckoes, are commonly associated with man; some of them live about primitive grass huts and also the thatched cabins of native canoes, while others occur about the walls and gardens of civilized man. Many geckoes are well adapted for overseas dispersal, dwelling about tidal wrack and depositing their hard-shelled eggs in drift wood. No attempt will be made to cite all the published records of geckoes on beaches and in tidal wrack. About seven species of geckoes occur in South Florida. The reef gecko (*Sphaerodactylus notatus*) was first discovered in Key West, Florida, and has since been found at various localities in Collier, Dade, and Monroe counties, as well as in the Bahamas and Cuba. It is generally considered to be an introduction; but its arrival in Florida may well have antedated that of civilized man. These tiny lizards have been found in tropical hammock and along beaches of the Florida Keys; they deposit their eggs about rocks and trash piles, and in driftwood logs. The ashy gecko (*S. cinereus*) has been taken on the Florida Keys, as well as in Haiti, Cuba, and the Isle of Pines. Although occurring in woods, it is more common about wharfs and buildings. I observed specimens about a ferry dock at Key West, where boats almost daily arrived from, and departed for, Havana. They were slipping in and out of cargo and stacked lumber on the wharf. It is easy to see how this diminutive lizard could have reached Florida as a stowaway. The ocellated gecko (*S. a. argus*), a native of Jamaica, may be established at Key West (Savage, 1954), but little is known of it there. The Mediterranean gecko (*Hemidactylus t. turcicus*) occurs in parts of Asia and Africa, as well as Cuba, Florida, and Yucatan. It is fairly abundant in edificarian situations on Key West, and has also been taken at Miami. The yellow-headed gecko (*Gonatodes fuscus*) was deliberately introduced into Key West by a reptile fancier in the 1930's. It still exists in certain edificarian situations there today. It ranges from Nicaragua to Colombia, and occurs on Cuba and Jamaica. Two other species of geckoes have been collected in Florida,

and at least one of them appears to be well established; their discoverers will doubtless report on them. For additional observations on Florida geckoes, see Carr (1940), Mittleman (1950) and H. M. Smith (1946). We may briefly discuss a few other geckoes sometimes found in saltwater habitats. *Aristelligella barbouri* of Great Inagua, British West Indies, lives in decaying wood and under the loose bark of dead sea-grapes and coconut palms. Its eggs are deposited beneath the bark of rotting palms (Noble and Klingel, 1932). *Gymnodactylus pelagicus* occurs on many islands of the Southwest Pacific; I found it common under driftwood logs on the beach at Port Moresby, Papua. *Lepidodactylus lugubris* occurs on many Pacific islands from the Philippines to Honolulu. It has been observed entering beached native canoes and laying its eggs therein (Snyder, 1917). For additional observations on its rather typical gekkonid life history, see Schnee (1901), Loveridge (1945), and Oliver and Shaw (1953). *Hemidactylus frenatus* has been found on boats in the Malay Peninsula (Boulenger, 1912). *Lygodactylus madagascariensis* ranges from the littoral zone to an altitude of 1,000 meters in Madagascar (Angel, 1949); and *Phelsuma lineatum* on the same island is equally common from the littoral zone to an altitude of 1,100 meters (Angel, 1950).

Brown and Alcalá (1957) studied the viability of lizard eggs exposed to sea water. The eggs of three Philippine geckoes (*Cosymbotus platyurus*, *Gehyra mutilata* and *Hemidactylus frenatus*) were quite resistant to salt water for at least 11 days and probably longer; but the eggs of a Philippine skink (*Dasia smaragdina*) could withstand no more than 3 to 5 days exposure to sea water.

Family XANTUSIIDAE.—The family Xantusiidae includes small, secretive, and nocturnal lizards. Its members are found at scattered localities from the southwest United States to Panama, with one representative on Cuba. The island night lizard, *Xantusia riversiana*, is confined to certain small, barren islands off the coast of southern California. The lizards occur under boulders almost at the water's edge; sometimes they feed upon marine isopods (Schwenkmeyer, 1949; Stebbins, 1954). Marine amphipods may also be eaten, and the stomachs of some individuals include bits of marine snail shells (Brattstrom, 1952).

SNAKES

Family BOIDAE.—The family Boidae (broadly considered) includes boas and pythons. A small Pacific boa (*Enygrus carinatus*) occurs on

most of the islands of the southwest Pacific. On Morotai Island, in the Moluccas, I found it to be common under masses of rooted coconuts at the bases of coconut trees growing supratidally. One specimen was found swimming in the sea at Natterer Bay, New Guinea (Loveridge, 1945, p. 114). An African sand boa (*Eryx jaculus*) was found beneath logs on and very near beaches in the vicinity of Bougie, Algeria (Bellairs and Shute, 1954). E. Ross Allen and I found several examples of a Cuban boa (*Tropidophis m. maculatus*) beneath debris at the edge of weed-grown tidal flats near Havana, Cuba. The ringed python (*Bothrochilus boa*), of New Guinea and the Bismarck Archipelago, resembles the sea-snakes (family Hydrophidae) in being laterally compressed; and like many sea-snakes, it is brightly ringed, at least when young. Loveridge (1945) stated that it hunts at night and feeds on rats and mice; however, in this he probably followed De Rooij (1917), who was sometimes in error in such matters. Its habits are virtually unknown, and it may prove to be aquatic. Near Lingayen, Luzon, Philippine Islands, I collected a reticulated python (*Python reticulatus*) in an abandoned cemetery on a sand dune near the sea. During a storm, large waves had dashed over the cemetery, washing out many of the burials and smashing concrete tombs. After abandonment, the entire cemetery and nearby dunes were thickly overgrown by coral-vine (*Antigonon*). Resting beneath the vine cover were many individuals of some caprimulgid bird, very similar in appearance to the American nighthawk. The python had eaten two of these birds.

Family ACROCHORDIDAE.—The family Acrochordidae, as defined by Schmidt (1949), includes but two species, both of them thoroughly aquatic. They are characterized by an absence of ventral plates, replacement of the usual snake head shields by small scales, and upwardly-directed nostrils on raised eminences of the snout. The karung or Indian water snake (*Acrochordus javanicus*) dwells about river mouths, and freely enters the sea (Loveridge, 1945, p. 126). It ranges from India to New Guinea; in the Malayan region it has been an important source of reptile leather (Ditmars, 1937). De Rooij (1917) made the remarkable statement that the karung eats water beetles and fruit. Such items were probably eaten by a fish, which was in turn devoured and digested by a karung, leaving undigested the vegetable matter and chitin (Neill and Allen, 1956). Loveridge (1945) stated that this snake is a fish-eater. The granular snake (*A. granulatus*; also called *Chersydrus granulatus*) is found from southeast Asia to

Australia. It is similar to its congener in habits, and likewise eats fish (Loveridge, 1945, p. 126). Tanner (1949) observed that the granular snake lives in either fresh or salt water, and feeds on small fishes. De Rooij (1917) stated that it inhabits rivers and the sea, feeding on fish. I collected a specimen in the salt water bay near the mouth of the Agno River at Lingayen, Luzon, Philippine Islands; it swam on the surface and refused to submerge even though I chased it about quite a while in a native dugout. Boulenger (1912) stated that the species had been found at sea in Malayan waters. The acrochordids represent an extreme of adaptation to marine life among the non-venomous snakes.

Family COLUBRIDAE.—The family Colubridae, the so-called "typical harmless snakes," includes about 275 genera, the vast majority of snakes. While many colubrids are completely non-venomous, others possess enlarged, grooved, venom-conducting teeth in the rear of the upper jaw. This is true of the colubrid sub-family Homalopsinae, which includes about 10 genera mostly specialized for aquatic life. Best known of the rear-fanged water snakes is the dog-faced water snake (*Cerberus rynchops*), found from India and the Philippines to northern Australia. On the north coast of Java it inhabits the intertidal zone, ditches of the tidal flats, and never emerges from the water (Kopstein, 1931). However, in some areas it will climb into the mangroves or other waterside bushes. Unlike the acrochordid water snakes and the venomous sea-snakes, it is capable of crawling rapidly when placed on land. Indeed, it has been known to leave the water and pursue mud-skippers (*Periophthalmus*) across the mudflats. Usually it remains in the water, where it preys upon eels and small fishes (Loveridge, 1945). I found this snake to be extremely abundant on flooded tidal flats near the mouth of the Agno River in Pangasinan Province, Luzon. It was observed at night when shallow water covered the flats. Most specimens were resting on the bottom, or in crab burrows, or about the submerged roots of halophytic palms. At higher tide the snakes disappeared, and the local Filipinos insisted that they went out into the deeper water in the middle of the channel. For additional observations see Boulenger (1912), De Rooij (1917), Gharpurey (1954), M. A. Smith (1943) and Taylor (1950).

Fordonia leucobalia, of the Australasian region, inhabits the intertidal zone, living in crab burrows and feeding upon crabs (Kopstein, 1931). It also eats fish, according to De Rooij (1917) and Boulenger (1912). According to the latter author, it is sometimes taken in fish-

ing stakes off the Malayan coast. Asiatic snakes of the homalopsine genera *Gerardia*, *Cantoria*, and *Bitia* all appear to be inhabitants of tidal rivers and coastal waters; *Enhydris bennetti* was caught at sea in the Straits of Hainan, in fishermen's nets (M. A. Smith, 1943). The capture of *E. bennetti* in the ocean, along with venomous sea-snakes, was also remarked on by Pope (1935). He thought the species was swept out to sea by freshets, and observed that another Chinese species of *Enhydris* inhabited fresh water, not salt. The Asiatic *Hipistis hydrinus* feeds on fishes and is often captured in fishing stakes (Boulenger, 1912; Cantor, 1847; De Rooij, 1917). In habits and coloration it is reminiscent of a sea-snake (hydrophid). The Asiatic *Erpeton tentaculatum* is remarkable in possessing two elaborate rostral appendages, the use of which is unknown. Locality records suggest that this snake frequents both fresh and brackish or salt water. There is a legend to the effect that it eats algae, but I have questioned the story (Neill and Allen, 1956). Nothing much seems to have been recorded about the habits of various other homalopsine snakes. Judging from locality records, some of the remaining species occur in fresh water, others in salt. The entire group is aquatic, and characterized by valvular nostrils and the "aquatic profile." De Rooij (1917) stated that all the species give birth to living young, as is true of most aquatic snakes. According to Ditmars (1936), the rear fangs of the homalopsine snakes convey a venom which rapidly paralyzes prey, allowing rapid deglutition even of spiny fishes. For additional notes, see Gharpurey (1954) and Kinghorn (1956).

Rear-fanged colubrids, other than the Homalopsinae, are customarily placed in the subfamily Boiginae. This is an artificial assemblage, the rear-fanged condition having evolved independently on a number of occasions. Nevertheless, the term is convenient. One boigine snake (*Macroprotodon cucullatus*) was found under stones in a supratidal zone near Bougie, Algeria; and another, tentatively identified as the Montpellier snake (*Malpolon monspessulanis*), was seen nearby (Bellairs and Shute, 1954). The so-called mangrove snake (*Boiga dendrophila*), found in south Asia and Indonesia, presumably inhabits mangrove swamps, at least occasionally. A vine snake (*Oxybelis aeneus*) was found in a bush near the sea at Los Blancos, El Salvador (Rand, 1957).

The remaining colubrid snakes, at least those of concern to us here, are characterized by simple, solid teeth; they comprise the subfamily Colubrinae, a cosmopolitan group of 170-odd genera. The Colubri-

nae have undergone adaptive radiation into terrestrial, subterranean, arboreal, and aquatic habitats. Some of the aquatic species dwell occasionally, and a few exclusively, in salt or brackish water. The water snakes (genus *Natrix*), especially, have succeeded in invading salt-water habitats.

The common water snake (*Natrix sipedon*) is found throughout most of the United States east of the Rockies. It has produced at least four brackish- or saltwater races, and six freshwater ones. Three of the saltwater forms occur in Florida. The mangrove water snake (*N. s. compressicauda*) is found on both coasts, from Hillsborough and Brevard Counties southward through the Keys; it has also reached the north coast of Cuba. Its tail, near the base, is slightly compressed laterally, presumably an adaptation toward aquatic life. However, it does not remain in the water at all times, but frequently climbs into mangroves and sometimes crosses roads (such as the Overseas Highway) in the vicinity of salt water. Its saltwater habitat has been mentioned by Allen and Neill (1952d), Allen and Slatten (1945), Barbour and Noble (1915), Barbour and Ramsden (1919), Clay (1938), Conant and Bridges (1935), and Schmidt and Davis (1941); aspects of its biology have been considered by E. R. Allen (1938b, 1941), Bishop (1940), Carr (1940), and Swanson (1948). It is largely nocturnal, and feeds upon fishes. Like other North American *Natrix*, it is a live-bearer. Mills (1950) found that it was killed by chemical mosquitociding in the Tampa Bay area, after having eaten rotenoned fish. Between Tampa Bay and Cedar Key, on the Florida west coast, the mangrove water snake intergrades with the Gulf salt-marsh snake (*N. s. clarki*); the latter ranges thence around the Gulf Coast into Texas. The habitat and habits of the Gulf saltmarsh snake have been discussed, or touched upon, by E. R. Allen (1938b, 1941), M. J. Allen (1932), B. C. Brown (1950), Cagle (1952), Carr (1940), Chamberlain (1937), Clay (1938), Conant and Bridges (1939), Guidry (1953), Haltom (1931), Liner (1954), and Viosca (1923, 1924, 1926, 1949). Toward the head of the Indian River, on the Florida East coast, the mangrove water snake intergrades with the Atlantic saltmarsh snake (*N. s. taeniata*); the latter is known only from Volusia, Brevard, and Indian River Counties. The Atlantic salt-marsh snake is not well known; its habits have been briefly mentioned by Carr and Goin (1942). The Atlantic and Gulf saltmarsh snakes resemble each other in being striped longitudinally, differing in this regard from the cross-banded or unicolor mangrove water snake.

As the common names suggest, the striped forms are essentially inhabitants of salt marsh, whereas the cross-banded one is characteristic of mangrove swamp. The striped forms are elusive and agile, the cross-banded one comparatively sluggish. Carr and Goin (1942) attempted to explain the similarity of *clarki* and *taeniata*, and their divergence from *compressicauda* which splits them apart geographically. They postulated that *compressicauda* developed on a Pleistocene island which preceded the Florida peninsula, and that a prototype of *taeniata* and *clarki* simultaneously developed along what was then the mainland. With the emergence of the peninsula, and the connection of the island with the mainland, the striped population was, of course, split into two groups, one on the Gulf and the other on the Atlantic.

All three races are somewhat affected by tidal rhythms, and generally forage when shallow tides are running over the flats or mangrove swamps. However, *compressicauda*, like the freshwater races of *N. sipedon*, is essentially nocturnal, and seldom forages by day even on favorable tides. The saltmarsh races, and especially *taeniata*, are less affected by the diel cycle and more by tidal rhythms. Indeed, near New Smyrna, Volusia County, on several occasions I observed *taeniata* foraging in broad daylight on favorable tides. *Clarki* is most abundant about glasswort (*Salicornia*) flats, but *taeniata* seems more characteristic of blackrush (*Juncus*) areas. As the tide first comes in, thousands of little fishes appear in the blackrush flats, in an inch or two of water. The densely clustered plant stems greatly inhibit the fishes' activity when trying to escape from an approaching saltmarsh snake; they flop about, butting into stems in a frantic effort to depart. *Taeniata* customarily takes advantage of these fish congregations among the *Juncus* stems, both by day and by night. It seems that the habits of this snake are specifically adapted to take advantage of the tidal rhythms.

Along the coast of Carteret County, North Carolina, is found the Carteret water snake (*Natrix sipedon engelsi*). Barbour (1943), Engels (1952), and Robertson and Tyson (1950) supplied what little is known of this snake; the remarks of Engels (1942, as *N. sipedon*) may apply to this race, also. So far as is known, the Carteret water snake frequents tidal creeks and brackish ponds on off-shore banks.

The freshwater races of *Natrix sipedon* occasionally venture into brackish habitats. This is true of the common water snake (*N. s.*

sipedon) in the Del-Mar-Va area (Conant, 1945), and of intergrades between this form and the banded water snake (*N. s. fasciata*) in Virginia (Werler and McCallion, 1951). The banded water snake and also the Florida water snake (*N. s. pictiventris*) are "occasional" in salt marsh, and the latter is "occasional" in mangrove swamp also (Carr, 1940).

The green water snake (*Natrix cyclopion*) appears to be somewhat more aquatic than the freshwater races of *N. sipedon*, and spends most of its time in the water. The eyes and nostrils are on the upper surface of the head, an adaptation to aquatic life. Two subspecies are known. *N. c. cyclopion* inhabits coastal areas from Alabama to Texas, and also the Mississippi Valley. It was taken by O. P. Allen (personal communication) in pools near the edge of Mobile Bay, and by M. J. Allen (1932) in brackish marshes of Harrison County, Mississippi. At both of these localities it was accompanied by *N. sipedon clarki*. Near Bay St. Louis, Mississippi, William E. Brode found it to inhabit brackish water almost exclusively. J. R. Dixon (personal communication) collected it in brackish water near Hackberry, Cameron Parish, Louisiana. On the Texas coast it is "equally abundant in fresh and brackish water." (Guidry, 1951, p. 52); and B. C. Brown (1950, p. 187) considered it "plentiful along the coast in the salt water marshes of eastern Texas." Conant and Bridges (1939) remarked on its occasional presence in brackish water. This subspecies appears to be confined largely to brackish habitats, except in the Mississippi Valley. Curiously enough, the more easterly race (*N. c. floridana*), found from Florida into South Carolina, has never been reported in saltwater areas, although it is even more thoroughly aquatic than its western ally. It seems to feed largely on pig-frogs (*Rana grylio*), while the western race eats both frogs and fishes. Differences in diet may explain why one race frequents, the other avoids, salt water.

The brown water snake, *N. t. taxispilota*, is the largest of its genus, reaching a length of seven feet. It inhabits the southeast United States, including most of Florida, being most characteristic of rivers, creeks, and backwaters. It forages in the water, mainly by night; the prey consists almost entirely of fishes, among which catfishes predominate. By day this snake usually lies in bushes overhanging the water; and it often follows rivers down to the limit of marginal woody vegetation. Along the lower Combahee River of South Carolina it was found in areas where the water was "salty and subject to extreme tidal fluctua-

tions, and where the associated aquatic fauna was made up mostly of marine species" (Neill, 1951b, p. 48). Specimens from this locality differed somewhat from inland *taxispilota*. Obrecht (1946, p. 73) mentioned the presence of *N. taxispilota* in tidal rivers and brackish waters of South Carolina. Jopson (1940) found it in herring nets set in tidal creeks near Georgetown, South Carolina. Recently I have observed this snake near the mouth of the Withlacoochee River, Levy County, Florida. The diamondback water snake (*N. t. rhombifera*) was found in a Texas rice canal, in fresh water but associated with numerous marine fishes upon which it preyed (Baughman, 1946). Mention has been made of the glossy water snake (*Natrix rigida*) in saltwater areas at the mouth of the St. Johns River. Specimens from this locality are completely black above, whereas most inland examples are greenish-gray with dorsolateral black stripes. Near Bay St. Louis, Mississippi, William E. Brode (personal communication) found Graham's water snake (*N. grahami*) in brackish marshes, where it fed upon breeding individuals of the pinewoods treefrog (*Hyla femoralis*). A water snake (*N. valida*) is confined to the west coast of Mexico and the southern tip of Baja California. Although essentially freshwater, it may invade the salt. The distribution suggests this; and one example was found under a canoe on a (sea?) beach (Conant, 1946). Some specimens of the Baja California population (*N. v. cелаeno*) had been feeding on mullet (*Mugil brasiliensis*), according to Van Denburgh (1896).

Guerin-Ganivet (1909) reported the common European water snake (*Natrix natrix*) in the sea along the Mediterranean coast; Hecht (1930) recorded it from the Baltic and North Seas. The latter author thought that it did not enter the ocean voluntarily, but was occasionally forced or frightened into the surf. However, he found that immersion in salt water had no harmful effects on the reptile. Loveridge (1945, p. 126) stated that this snake had been found swimming in the English Channel far from land. M. Smith (1951, p. 227) mentioned a specimen caught in the Bay of Biscay many miles from shore, and "none the worse for its immersion in salt water." Another Old World species, the viperine water snake (*N. maura*), was found among stones on the beach near Bougie, Algeria (Bellairs and Shute, 1954).

The black swamp snake (*Seminatrix pygaea*) is found from South Florida north into South Georgia and the coast of the Carolinas. A dwarfed ally of the water snakes, it is generally a burrower amid

clustered aquatic plants or in soggy debris about pond margins. Although essentially an inland species, it has been found in salt marsh near Bluffton, Beaufort County, South Carolina, and also near Panama City, Bay County, Florida (Neill, 1951b, p. 52). Dowling (1950, p. 14) mentioned a specimen from three miles east of Savannah, Chatham County, Georgia; this locality appears to be salt marsh, also. The aforesaid Georgia and South Carolina specimens are referred to the subspecies *S. p. paludis*; the Florida one cannot be allocated subspecifically.

The common garter snake (*Thamnophis s. sirtalis*) of the eastern United States was found on the beach near Bluffton, Beaufort County, South Carolina, where it was associated with the island glass-lizard (*Ophisaurus compressus*) and fiddler crabs (*Uca*). Many specimens were seen in dry patches of dune grasses, and about damp tidal wrack. A colony of these snakes was also found near the mouth of the Steinhatchee River, Dixie County, Florida. Specimens from this locality were of unusual coloration; the venter was blue, the dorsum black with blue stripes. Curiously enough, with these unusual garter snakes were found ribbon snakes (*T. sauritus*), likewise remarkable for a blue venter and a blackish, blue-striped dorsum. The situation merits further study. More or less typical Florida ribbon snakes (*T. sauritus sackeni*) have been found in salt marsh at Merritt Island, as noted previously; and also at Cedar Key, Levy County, Florida. Carr (1940, p. 23) listed this reptile as "occasional" in Florida salt marsh. The western ribbon snake (*T. s. proximus*) was found by me about pools of the salt marsh near Sabine Pass, Jefferson County, Texas. It was collected by J. R. Dixon (personal communication) from salt marsh near Hackberry, Cameron Parish, Louisiana. Specimens from this habitat were of unusual coloration, and distinguishable from those taken farther inland.

As noted previously, the striped swamp snake (*Liodytes alleni*) was found at Merritt Island; and a species of *Helicops* (a tropical ally of *Liodytes*) was carried into the bay at the mouth of the Orinoco River in floating masses of water-hyacinth (Archie F. Carr, personal communication).

The redbellied mud snake (*Farancia a. abacura*) is a large, muck-burrowing reptile of the southeastern United States. Throughout most of its range it dwells in freshwater bogs, ponds, and swampy streams, feeding almost exclusively upon the big salamanders, *Amphiuma* and *Siren*. However, in coastal Georgia and South Carolina it inhabits

inlets, estuaries, salt creeks, and salt marshes, feeding upon fishes. This coastal population may represent an unnamed subspecies (Neill, 1951b, pp. 49-50). E. Ross Allen and I found a specimen about 30 yards from the ocean at Ponte Vedra Beach, St. Johns County, Florida; it was not especially different from inland examples. A western race (*F. a reinwardti*) was found by me in salt marsh near Sabine Pass, Jefferson County, Texas.

The rainbow snake (*Abastor erythrogrammus*) is closely related to the redbellied mud snake. It is found in streams, especially neutral or alkaline ones, being characteristic of calcareous spring runs. The adults feed almost exclusively upon the eel (*Anguilla bostoniensis*). This snake is found in the salt water at the mouth of the St. Johns River, and also about Choctawhatchee Bay in Walton County, Florida. The two saltwater populations, in spite of their geographic separation, resemble each other and diverge from the norm of inland specimens. The usual rainbow snake is black with red stripes dorsally, pink or red (with black spots) ventrally, and yellow sublaterally. In most saltwater examples the red is of a deeper hue, and replaces the yellow which is completely lacking. Richmond (1945) found the species in tidal marshes of the Chickahominy River in Virginia, at a locality where there was considerable tidal fluctuation and where the water became slightly brackish during times of drought.

The western ringneck snake (*Diadophis amabilis*), a diminutive, secretive reptile of the western United States, has been found in salt marsh about San Francisco Bay (Stebbins, 1954).

The indigo snake (*Drymarchon corais couperi*), found from Florida northward to southern Alabama and Georgia, is a large terrestrial species. It feeds upon almost any vertebrate that it can catch and master. According to Carr (1940), it is occasional in salt marsh and mangrove swamp of Florida.

The rough green snake (*Opheodrys a. aestivus*) is an arboreal, insectivorous snake of the southeast United States. On the Florida Keys it is common in supratidal vegetation. Carr (1940, p. 25) listed it as occasional in mangrove swamp of Florida.

The common hog-nosed snake (*Heterodon platyrhinos*) of the eastern United States feeds almost exclusively upon toads, and so is confined to areas where these amphibians are common. According to Kauffeld (1942), in the vicinity of New York City, beaches and sand dunes are its "favorite habitat."

The leaf-nosed snakes (genus *Phyllorhynchus*) are small, secretive

reptiles inhabiting arid regions of the southwest United States and northwest Mexico. The Mexican leaf-nosed snake (*P. d. decurtatus*) has been found at night on the beach of San Carlos Bay near Guaymas (Klauber, 1935b). Another species (*P. arenicola*) is known only from dunes along the beach of Isla Monserrate, Baja California (Savage and Cliff, 1954). A Mexican patch-nosed snake (*Salvadora mexicana*) was found in palm fronds making up the roof of a salt-drying vat near the beach in Michoacán, Mexico (Peters, 1954). A parrot snake (*Leptophis m. mexicanus*), an arboreal species, was found "in a small tree near the seashore" at the mouth of the Río Barranca, Puntarenas Province, Costa Rica (Taylor, 1954, p. 717).

The blacksnake (*Coluber constrictor*) is a familiar reptile in the United States. Found in brushy places generally, it feeds upon a wide variety of small organisms, both vertebrate and invertebrate. Obrecht (1946, p. 73) found the northern blacksnake (*C. c. constrictor*) to be abundant amid tall grasses of the coastal dune region at Myrtle Beach State Park, Horry County, South Carolina; and T. H. Lewis (1946) reported it from salt marsh on Smith Island, North Carolina. Carr (1940) considered the southern blacksnake (*C. c. priapus*) to be "occasional" in salt marsh of Florida. An Old World relative of the blacksnake, the horseshoe snake (*C. hippocrepis*) was found in a supratidal situation near Bougie, Algeria (Bellairs and Shute, 1954). The Clarion Island racer (*Masticophis anthonyi*) inhabits one island in the Revillagigedo group, about 210 miles southwest of the tip of Baja California. It occurs on coral and lava beach as well as farther inland, dwelling about sea-bird colonies and cactus patches (Slevin, 1926). It may eat young boobies (Ortenburger, 1928). One specimen had eaten a hatchling of the Pacific loggerhead (Brattstrom, 1955). This snake is unusually fat and oily, for a racer (Ortenburger, 1928).

The rosy rat snake (*Elaphe guttata rosacea*) is confined to the Florida Keys. Although more common on the ground or about piles of debris, it sometimes climbs into supratidal vegetation; it has been found in mangroves. Deckert's rat snake (*E. obsoleta deckerti*), confined to the Keys and the extreme southern tip of the mainland, is a more arboreal snake, and is "frequent" in mangrove swamp (Carr, 1940, p. 25). Conant and Bridges (1939, p. 61) stated that it "lives in the tangled undergrowth on the inland side of the mangrove swamps which partially or wholly fringe the islands it inhabits. Here it forages for mice or climbs in search of birds and their eggs." The

yellow rat snake (*E. o. quadrivittata*) was noted by me in bushes along the lower reaches of the Sikehatchie River in South Carolina, where tidal fluctuations were pronounced and the aquatic fauna consisted largely of marine species. The snake also occurs on certain North Carolina coastal islands, perhaps in supratidal situations (Engels, 1952). The Everglades rat snake (*E. o. rossalleni*), although usually arboreal, enters treeless salt marsh (Allen and Neill, 1950c). All of these rat snakes, when adult, feed upon rodents and birds.

The Florida kingsnake (*Lampropeltis getulus floridana*) is a large, terrestrial reptile, most characteristic of wooded areas near water. It feeds upon a wide variety of vertebrate organisms. Carr (1940) listed it as "occasional" in salt marsh. A close ally, the speckled kingsnake (*L. g. holbrooki*) was found to be as common in the salt marsh as in the woods of southeastern Texas (Guidry, 1953, p. 51); and E. Ross Allen and I collected a specimen of this snake on the causeway across Mobile Bay, Alabama, in supratidal vegetation. J. R. Dixon (personal communication) found this snake in salt marsh near Hackberry, Cameron Parish, Louisiana. Specimens from that habitat were of unusual coloration, the venter being black and orange rather than the usual black and yellow.

The genus *Tretanorhinus* includes a number of neotropical species, all of them aquatic so far as is known. The Cuban cativo (*T. v. variabilis*) is an inhabitant of streams. It forages by night on the bottom or in the shallows, preying upon small fishes. At Playa de Rosario, Habana Provincia, Cuba, E. Ross Allen and I found it to be common in salt marsh, about old docks, and at the mouths of drainage ditches opening into the sea. Grant ("1946") found one cativo in a brackish tidal estuary at Rancho Gavilán, Cienfuegos, Cuba; he considered it to represent a distinct species, which he named *T. gaigeae*. The Cayman Island race (*T. v. lewisi*) has been found in small, natural or excavated wells, often brackish from ocean seepage (C. B. Lewis in Grant, 1940b, pp. 47-48). A Central American species (*T. nigroluteus*) is mainly or exclusively an inhabitant of mangrove swamp (Barbour and Amaral, 1924; Taylor, 1951).

A small Jamaican snake (*Dromicus funereus*) was found near Montego Bay, under piles of coconuts, in association with a lizard (*Celestus occiduus*), a frog (*Eleutherodactylus jamaicensis*), slugs, land crabs, and spiders (Grant, 1939). This may well have been in a supratidal situation. Examples of a Cuban species (*D. andreae*), collected about a brackish lagoon near Guantánamo Bay, were larger

than those collected farther inland (Barbour and Ramsden, 1919). Closely allied to *Dromicus* is the genus *Alsophis*, with representatives on many Antillean islands. The Cuban racer (*A. a. angulifer*) was found by E. Ross Allen and myself on the sandy, rock-strewn beach at Punta Brava, Habana Province, Cuba; and another species (*A. antillensis*) "is most readily found at early morning along the beaches" of Tortola Island (Grant, 1932b, p. 345).

Family ELAPIDAE.—The elapids are venomous snakes found in both the Old World and the New. Most elapids are terrestrial, fossorial or arboreal; a few dwell about fresh water. The Indian cobra (*Naja naja*) is an adaptable, essentially terrestrial species, occurring in woods, jungle, fields, gardens and edificarian situations of southern Asia. It enters the water readily, and has been observed swimming in the sea (Gharpurey, 1954, p. 54). The Australian black snake (*Pseudechis porphyriacus*) has been found swimming in the middle of Botany Bay; the Australian taipan (*Oxyuranus scutellatus*) is abundant around the shores of the Gulf of Carpentaria; and other Australian elapids (species not named) may swim across estuaries (Kinghorn, 1956).

Family HYDROPHIDAE.—The family Hydrophidae includes forty-odd species, all of them aquatic. Semper's sea-snake (*Hydrophis semperi*) inhabits the fresh waters of Lake Bombon (often miscalled Taal from the name of the volcano which arises from it) on Luzon, Philippine Islands; and Crocker's sea-snake (*Laticauda crockeri*) is confined to brackish Lake Tungano on Rennell Island in the Solomons; but the remaining species are all marine. The sea-snakes are eel-like in build, with a vertically flattened, oarlike tail. Some of them never exceed two or three feet in length, although the bluebanded sea-snake (*Hydrophis cyanocinctus*) attains a length of about nine feet. The family consists of two subfamilies. The members of the Laticaudinae are characterized by the presence of ventral shields (crawling plates); they are oviparous, and venture onto rocky island shores for breeding. The members of the subfamily Hydrophiinae, in contrast, completely lack ventral shields; they give birth to living young at sea, and never venture onto the land. All of these snakes are venomous, and most of them exceedingly so. The venom is neurotoxic, and serves to paralyze eels, spiny fishes, or other prey. According to De Rooij (1917), crustaceans may also be eaten by some species. In the Philippines, certain hydrophid snakes feed upon small eels of the families

Ophichthyidae, Myridae, and Moringuidae; and are in turn fed upon by large moray eels. According to Breder (1949), certain eels are "mimics" of sea-snakes. Clusters of barnacles are sometimes found on sea-snakes (Taylor, 1950). Sea-eagles (*Haliaeetus leucogaster*) feed upon sea-snakes in Malayan waters (Gibson-Hill, 1949). In the southwest Pacific there are quite a few fatalities from sea-snakes. Most victims are fishermen who netted or otherwise molested these reptiles; sea-snakes rarely if ever attack bathers.

Man is an important predator on certain of the species. The reptiles are eaten, or valued as medicine, in parts of the Orient, and are taken in large quantities by Japanese fishermen. The larger kinds are valued for leather; at one time the Philippine government attempted to regulate the sea-snake industry, in order to prevent the leather-producing species from being exterminated.

Remarkable aggregations of sea-snakes have been reported, especially in Philippine waters; W. P. Lowe (1932, p. 43) once saw "millions."

Hydrophids, with the exception of one species, are confined to the Old World, being most characteristic of warm shallow seas and river mouths of the Indo-Australian region. The sole exception is the yellow-bellied sea-snake (*Pelamydrus platurus*); it ranges from Madagascar northward to Siberia, and eastward to (but not into) eastern Polynesia; and also has a large population on the Pacific coast of the New World from northern South America to Tiburón Island, in the Gulf of California off the coast of Sonora, Mexico. It is especially common about the Pacific end of the Panama Canal, and there have been rumors —apparently unfounded— that it has made its way through the canal into Atlantic waters (Ditmars, 1936). New World specimens do not differ noticeably from Old World ones; and Taylor (1951) once suggested that the snake might have crossed the Pacific as a stowaway in Spanish ships which once plied the waters between Manila and Mexico or Central America. However, Taylor (1953) later noted that the earliest white explorers found this species in abundance off the coast of Central America.

For further remarks on the habits of sea-snakes, consult Barbour (1926), Barrett (1950), Ditmars (1937), Elton (1948), Gibson-Hill (1949), Herre (1942), Herre and Rabor (1949), Klauber (1935a), Myers (1945), Slevin (1935), Smith and Taylor (1945), M. A. Smith (1943), Stejneger (1907), Taylor (1922a, 1950), Tweedie (1949), and Wall (1908). M. A. Smith studied the taxono-

my and distribution of the entire group, and provided some notes on habits.

Family VIPERIDAE.—The viperids are venomous snakes of the Old World. One species, the common viper (*Vipera berus*), while essentially terrestrial, swims readily and has been found many miles at sea off the coast of Ireland (M. A. Smith, 1951).

Family CROTALIDAE.—Snakes of the family Crotalidae are called pit-vipers. The cottonmouth moccasin (*Agkistrodon p. piscivorus*) is probably the commonest pit-viper within its range. It is found in the Atlantic Coastal Plain from South Florida to southeastern Virginia; in the Gulf Coastal Plain from Florida to the Rio Grande River of Texas; and in the Mississippi Valley northward to southern Illinois. The cottonmouth is a large, venomous snake, semiaquatic, and seldom encountered at any distance from water. It is common about river swamps, pond margins, the Everglades "prairies," and low, swampy places generally. It is also abundant on some of the Gulf Islands in Suwannee Sound, where there is no permanent fresh water (Carr, 1937a). Here it frequents a supratidal plant association (mostly red mangrove and shore bay), feeding upon birds, a skink (*Eumeces inexpectatus*), and marine fishes (including *Cyprinodon variegatus* and an atherinid, probable *Menidia*). Allen and Swindell (1948) and Allen and Neill (1950b) also noted the presence of this species on islands off the Florida coast. Peterson *et al.* (1952) found it in brackish water on the Florida Keys. I collected a large specimen in salt marsh at Cape San Blas, Gulf County, Florida. The species was found to be fairly common along the lower Salkehatchie River of South Carolina, in areas where the associated aquatic fauna was mostly of marine species. J. Bailey (*in* Engels, 1952) saw a cottonmouth in a brackish pond on the Shackleford Banks, North Carolina; and in southeast Virginia, the species is common in "vast bayside swamps along the barrier beach. . . separated from the mainland by a series of brackish bays" (Wood, 1954, p. 159).

The family Crotalidae also includes the rattlesnakes, genera *Sistrurus* and *Crotalus*. The dusky pygmy rattlesnake (*Sistrurus miliarius barbouri*) and the eastern diamondback rattlesnake (*Crotalus adamanteus*) are "occasional" in the salt marsh of Florida, according to Carr (1940). The latter species was reported on Cudjoe Key, Florida, by Allen and Slatten (1945). At this locality, and elsewhere in the Keys, it sometimes dwells in crab burrows. Conant and Bridges

(1939, p. 146) stated that the diamondback "even crosses salt-water, as when it travels from the mainland to the Florida Keys along the coast. On some of the Florida Keys it is extraordinarily abundant." On one occasion a diamondback was found swimming at sea, about 22 miles off the coast of Tampa, Florida (E. Ross Allen, personal communication). Loennberg (1894) mentioned that diamondbacks swam from key to key in Florida. In south Gulf and Franklin Counties, Florida, the eastern diamondback rattlesnake is more common in salt marsh than in any other habitat; and in many parts of the state it is frequently found in scrubby supratidal vegetation. Near Bluffton, Beaufort County, South Carolina, I found it in patches of dune grasses, and even about debris of the tidal wrack zone. It is a good swimmer, and has been reported swimming in the ocean several miles from land. Clench (1925) found a large diamondback on a mass of water hyacinth which drifted onto Sanibel Island, Lee County, Florida, from the mainland, following a flood on the Caloosahatchee River. According to Klauber (1949, p. 94), the eastern diamondback is often found swimming at considerable distances off the Florida coast, and the western diamondback (*C. atrox*) likewise off the Texas coast; rattlesnakes (species not specified) are occasionally found floating in the Pacific a short distance off shore. J. R. Dixon (personal communication) found seven western diamondbacks in salt marsh about 15 miles below Palacios, Matagorda County, Texas; the snakes were resting atop halophytic rushes and grasses. The El Muerto Island rattlesnake (*C. mitchelli muertensis*), confined to one island in the Gulf of California, inhabits rocky areas including boulder-strewn beaches. One specimen was found moving inland to escape the tide (J. R. Slevin in Klauber, 1949). In a study of rattlesnake biology, Klauber (1956, p. 469) cited a number of papers dealing with the occurrence of these reptiles in salt water. Species included were the eastern and western diamondbacks, the red rattlesnake (*C. ruber*) of California, and the southern Pacific rattlesnake (*C. viridis helleri*).

THE TUATARA

The accounts of species may be closed with the tuatara (*Sphenodon punctatus*), sole surviving member of the ancient reptile order Rhynchocephalia. This primitive species, superficially iguana-like in appearance, is today confined to 13 small islands off the coast of

New Zealand. Its habits on Karewa Island were studied by Schmidt (1953a). The surface of this island is honeycombed with nesting burrows of a mutton-bird (*Puffinus carneipes*). The tuatara also inhabits these burrows, which are dug into a humus-like soil. This soil is derived mostly from plant debris, especially the leaves of a coprosma. The *Sphenodon-Puffinus-Coprosma* association appears to be a climax condition. The tuataras are excellent swimmers, and will take readily to water, either fresh or salt; they can remain submerged for a long while (F. N. Blanchard, 1924). Fishes are sometimes eaten, but form an insignificant portion of the diet. For further observations on this "living fossil" and its environment, see F. C. Blanchard (1936), Dawbin (1949), Schmidt (1952), and Sladden (1924).

DISCUSSION AND SUMMARY

Evidently, amphibians and reptiles invade saltwater areas much more often than has generally been realized.

Among amphibians, salamanders are poorly adapted to withstand salt. The few species occasionally found in saltwater habitats mostly belong to the related families Salamandridae and Ambystomidae. One European salamandrid (*Triturus helveticus*) has been reported several times in brackish water; and a Mexican ambystomid (*Ambystoma subsalsum*) is confined to a salt lake. Salamander families apparently unreported from saltwater areas are the Hynobiidae, Cryptobranchidae, Amphiumidae and Proteidae. Of these, the proteids are aquatic species with delicate skin and external gills; the Cryptobranchidae includes only three species, all aquatic and generally characteristic of upland streams; the Amphiumidae includes but one species, an aquatic muck-burrower; the Asiatic hynobiids are few in number and largely confined to the vicinity of upland brooks, so far as is known. The absence of these families from saltwater habitats is not surprising.

Frogs have been more successful in invading saltwater associations; many of the Ranidae, Bufonidae and Hylidae do so casually, and a few species (such as *Rana cancrivora* of Asia, *R. pipiens sphenoccephala* and *Acris gryllus paludicola* of the United States, and *Bufo calamita* and *R. ridibunda* of Europe) apparently thrive in supratidal situations. The microhylid *Gastrophryne carolinensis* also occurs in saltwater habitats with considerable frequency. Frog families apparently unrepresented in saltwater areas include the Liopelmidae, with a single species in New Zealand; the Ascaphidae, with a single species in the Rocky Mountains of the United States; the Rhaco-

phoridae, composed mostly of tropical, arboreal species; the Rhinophrynidae, confined to Mexico; the Centrolenidae, tiny frogs of the New World rainforest; the Brachycephalidae, also of the New World rainforest; the Pelobatidae; and the Discoglossidae. Further collecting is apt to turn up some of the pelobatids and discoglossids in saltwater habitats.

The caecilians (Order Gymnophiona), representing a third major group of the Amphibia, have not been observed in saltwater habitats, but this is not surprising; for caecilians in general are burrowers in the leafmold of tropical forests, and only one species is known to be aquatic.

Among turtles, two families (Cheloniidae and Dermochelyidae) are composed of saltwater species, highly adapted for marine life; and one genus (*Malaclemys*) of the Emydidae is mostly confined to the intertidal and middle neritic zones. Freshwater turtles seem very apt to invade haline situations; members of such diverse families as the Chelydridae, Kinosternidae, Emydidae and Trionychidae have all been encountered in saltwater habitats. The single carettochelyid species may be largely saltwater, not freshwater as generally believed. Some essentially terrestrial turtles, of the Testudinidae and Emydidae, occasionally venture into the supratidal zone. The only turtle families apparently unreported from saltwater areas are the Dermatemydidae, which includes but a single species; the Platysternidae, likewise including but one species and it montane; and the Chelyidae or snake-necked turtles. The last family is represented in the tropics of South America, Australia and New Guinea. The apparent absence of chelyids from saltwater habitats is apt to be illusory, the result of incomplete collecting. The South American mata-mata (*Chelys fimbriata*) and some Australian and New Guinean species of *Emydura* and *Chelodina* are to be expected in such areas.

Crocodylians have been moderately successful in haline situations. The estuarine crocodile (*Crocodylus porosus*) thrives about the intertidal and middle neritic zones, and does not hesitate to venture into lower neritic and oceanic waters. The American crocodile (*C. acutus*) also appears to be most characteristic of haline habitats. Among the alligatorids, the American alligator (*Alligator mississippiensis*) and the brown caiman (*Caiman sclerops fuscus*) often invade coastal marshes. The only crocodylian family seemingly unreported from salt water is the Gavialidae, represented by a single species of India. This species, the gavial (*Gavialis gangeticus*), should follow the Ganges

River downstream into brackish water. Perhaps the heavy settlement of the Ganges Delta has extirpated the species from that area.

Among lizards, gekkonids often occur in the supratidal and tidal zones; many of the species are adapted for overseas dispersal. The Iguanidae has produced the marine iguana (*Amblyrhynchus cristatus*) of the Galapagos, a species deriving its sustenance entirely from the sea. The iguanids also include numerous species occasionally invading supratidal situations; and a few, such as the Cuban *Leiocephalus carinatus*, are largely beach dwellers. A distinctive saltmarsh iguanid (*Anolis carolinensis* subspecies) inhabits the southwest coast of Florida. The Agamidae has produced a few casual invaders of saltwater habitats. A xantusiid (*Xantusia riversiana*) is confined to small islands and ventures into the supratidal and tidal wrack zones. Two scincids (*Dasia smaragdina* and *Ophiomorus blanfordi*) may be characteristic of the supratidal zone; and another scincid (*Emoia atrocostatum*) is thoroughly adapted for beach life, relying on the sea for food and shelter. Perhaps *Emoia nigrum* is also a beach species. Several other scincids frequent tidal wrack, and like so many gekkonids, are adapted for overseas dispersal. Some lacertids occasionally turn up in haline situations, and *Acanthodactylus cantoris* may be characteristic of such. The Teiidae has produced the caiman lizard (*Dracaena guianensis*), which may subsist exclusively on brackish-water mollusks. An anniellid (*Anniella pulchra*), an amphisbaenid (*Trogonophis weigmanni*), a varanid (*Varanus salvator*), and an anguid (*Ophisaurus compressus*) seem to do especially well in saltwater areas; and the anguid *Diploglossus millepunctatus* is dependent on the sea for existence. Lizard families seemingly unreported in saltwater areas include the Dibamidae, Feyliniidae, and Anelytropodidae, all composed of degenerate, superficially worm-like burrowers; the Gerrhosauridae, characteristic of rocky hills and upland savanna; the Pygopodidae, mostly burrowers or grassland dwellers with degenerate limbs; the Helodermatidae, composed of but two species; the Xenosauridae, also of two species; the Shinisauridae, of one species; the Cordylidae, mostly desert lizards; and the Chameleontidae, mostly slow-moving arboreal species. The general absence of these families from saltwater areas is not surprising.

Snakes have been successful in saltwater habitats. The family Hydrophidae is almost exclusively marine, its members highly adapted for sea life; the snakes of the family Acrochordidae, and those of the colubrid subfamily Homalopsinae, are likewise generally marine.

These reptiles are mostly to be found in neritic waters. Among other colubrid subfamilies, the Colubrinae has produced a number of species invading mangrove swamp or saltmarsh. In fact, most of the semiaquatic colubrine snakes of Florida (genera *Thamnophis*, *Lioodytes*, *Seminatrix*, *Natrix*, *Farancia* and *Abastor*) are found in saltwater habitats at least occasionally; and, as noted, there are several distinct saltwater races of *Natrix sipedon*. Some Neotropical colubrids of the genus *Tretanorhinus* also have been successful in salt water. Two crotalid species, the cottonmouth (*Agkistrodon piscivorus*) and the eastern diamondback rattlesnake (*Crotalus adamanteus*), are often found in supratidal plant associations. Snake families apparently lacking from saltwater habitats include the Typhlopidae, Leptotyphlopidae and Anomalepididae, all of them tiny, superficially worm-like burrowers; the Uropeltidae, Xenopeltidae, and Anilidae, all primitive snakes of tropical rainforest; and the Amblycephalidae, the members of which feed upon slugs. The absence of these reptiles from saltwater areas is not remarkable. It is, however, difficult to explain why the large family Elapidae appears to be so poorly represented in haline situations. Of course, the majority of elapids inhabit the Australasian region, which is poorly known ecologically.

The tuatara (*Sphenodon punctatus*), while venturing just occasionally into salt water, is a part of an association which is intimately dependent upon the sea for its continued existence.

MacGinitie (1939: 30-31) stated, "Practically no extensive studies have been made of sandy beaches." Davis and Williams (1950: 519) commented, "Scientifically, the waters of the mangrove areas of the world remain practically unexplored." No doubt further study will reveal many more amphibians and reptiles in saltwater habitats.

Apparently, in North America and Europe, a relatively high percentage of the total herpetofauna has been taken in saltwater situations. However, this circumstance probably reflects herpetological activity in these countries; Asia, Africa and the Australian region should yield many more species in supratidal, tidal wrack, intertidal and middle neritic zones.

Florida has an extraordinarily large number of amphibians and reptiles in saltwater areas. Probably this circumstance does not reflect intensive collecting; for, while the state has attracted the attention of many herpetological collectors, the haline habitats have generally been neglected. In the opening remarks of this paper, it was suggested that the geological history of Florida has favored the invasion of

saltwater situations by essentially freshwater or inland amphibians and reptiles. If the suggestion is correct, one might expect similar invasion by other groups of organisms. In this connection, Berner and Sloan (1954) reported the larvae of various damsel flies and mayflies, as well as adult water-striders, in brackish waters of Florida, the species involved being freshwater ones. Odum (1953) has also remarked on the interchange of fresh- and saltwater organisms in Florida.

Apparently, amphibians and reptiles become modified anatomically and/or physiologically in response to life in saltwater habitats. Saltwater populations of essentially freshwater or inland species are apt to exhibit unusual coloration. This is true, for example, of the leopard frog (*Rana pipiens*), which was very dark in the mangrove swamps of Southwest Florida; of the Gulf Coast toad (*Bufo valliceps*), which was blackish in certain coastal marshes of Louisiana; of the Pacific tree-frog (*Hyla regilla*), which displayed an unusual head pattern on Cedros Island off the Baja California coast; of the American alligator (*Alligator mississippiensis*), which was notably bright colored about the Florida Keys; of the brown water snake (*Natrix taxispilota*), which on the South Carolina coast displayed small X-shaped blotches rather than the normal square ones; of the glossy water snake (*N. rigida*), which was unusually blackish at the mouth of the St. Johns River in Florida; of the black swamp snake (*Seminatrix pygaea*), which displayed a red (rather than a red and black) venter in a salt marsh of Bay County, Florida; of the common garter snake (*Thamnophis sirtalis*), which, near the mouth of the Steinhatchee River, Florida, was black with sharply defined blue stripes; of the ribbon snake (*T. sauritus*), which was also blackish with blue stripes in the Steinhatchee area; of the rainbow snake (*Abastor erythrogrammus*), which was black and deep red in saltwater areas as opposed to black, pink and yellow in freshwater ones; of the speckled kingsnake (*Lampropeltis getulus holbrooki*), which in the salt marsh of Cameron Parish, Louisiana, was black and orange (rather than black and yellow) below; and of the eastern diamondback rattlesnake (*Crotalus adamanteus*), which displayed an unusually bright black-and-yellow pattern on the Florida Keys.

Saltwater races of essentially freshwater or inland species likewise are divergent from the parent stock in coloration. Thus the Key mud turtle (*Kinosternon b. bauri*) is characterized by a blackish coloration with reduced but more intense yellow striping; the anole (*Anolis carolinensis* subspecies) of the Southwest Florida salt marshes has a

green rather than a red throat-fan; the mangrove water snake (*Natrix sipedon compressicauda*), banded posteriorly, is generally striped anteriorly and frequently is uniformly reddish-orange, whereas the freshwater races of *N. sipedon* are cross-banded or blotched; the two saltmarsh snakes (*N. s. clarki* and *N. s. taeniata*) are completely striped; the Key blacksnake (*Coluber constrictor haasti*) is at any age unusually dark for its species; and the cricket frog (*Acris gryllus paludicola*) of the Texas salt marsh is uniformly pinkish or reddish, rather than variegated with green and black as is commonly the case with inland races.

In general, and with a few exceptions, residence in salt water seems to result in a deepening or intensification of yellow, orange or red pigment; an intensification of black pigment but not at the expense of red areas; and the development or intensification of a lineate pattern. At present it would be premature to suggest which of these trends result from natural selection and which from some environmental effect on the phenotype, although of course a lineate pattern is not apt to be purely phenotypic.

Residence in salt water may also bring about structural modifications. For example, in three saltwater races of the water snake (*Natrix sipedon clarki*, *N. s. compressicauda*, and *N. s. taeniata*), the base of the tail is vertically flattened to a slight degree. Presumably this makes for more efficient swimming. Nevertheless, these snakes spend a good bit of their time out of water, on mangrove branches or tussocks of *Juncus* and marsh grasses; they are no more aquatic than their freshwater relatives without flattened tails. The spotted turtles (*Clemmys guttata*) were unusually small in brackish marshes of Maryland, and unusually rough-shelled in some areas of brackish water. These modifications are apt to be of environmental origin. Thoroughly marine reptiles, such as the sea turtles and hydrophid snakes, display striking anatomical, physiological and behavioral modifications. These have been described by Barbour (1926), Carr (1952), Daniel and Smith (1947), Deraniyagala (1930a, 1933, 1936b), Ditmars (1937), Herre (1942), Hooker (1908a, 1908b), Loveridge (1945), Myers (1945), Oliver (1946), Pope (1939, 1955), M. A. Smith (1926), Wall (1908) and Williston (1914), and need not be summarized here.

Essentially freshwater or inland species usually must alter their diets when dwelling in saltwater habitats. It is not surprising to find normally insectivorous frogs and lizards feeding upon small crabs.

amphipods and isopods in supratidal areas; or the American alligator eating shrimp, crabs, mullet and menhaden in brackish marshes. However, some dietary modifications, imposed by residence in salt-water habitats, are quite remarkable. Thus, Graham's water snake (*Natrix grahami*) usually feeds upon crayfishes, but in Mississippi salt marshes it ate pinewoods treefrogs (*Hyla femoralis*). The redbellied mud snake (*Farancia abacura*) normally feeds upon large salamanders, but in coastal marshes of South Carolina it eats fishes. The common snapping turtle (*Chelydra s. serpentina*) in fresh water feeds upon many aquatic animals and some plant material, but in a Massachusetts salt marsh it subsisted entirely upon a halophytic grass (*Distichlis*). The striped swamp snake (*Liodytes alleni*) and the chicken turtle (*Deirochelys reticularia*), in freshwater areas, feed upon crayfishes; but in saltwater habitats they must accept some other prey. Methods of foraging must likewise be modified; and in some cases tidal rhythm, rather than the diel cycle, has come to control activity.

Saltwater amphibians and reptiles merit much further study, from the standpoints of taxonomy, physiology, ecology and animal behavior.

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